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POSTGLACIAL MIGRATION OF FORESTS IN ILLINOIS, WISCONSIN, AND MINNESOTA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 454

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(WITH FIFTEEN FIGURES)

Introduction

The migration of biota initiated by the retreat of the Pleistocene ice sheets has long attracted the attention of investigators, especially ADAMS (**3, 4, 5**), GLEASON (**19**), HARSHBERGER (**20**), BRAUN (**7**), and TRANSEAU (**35**). The Pleistocene in North America lasted approximately one million years, in which time the northern half of the continent was glaciated during four distinct periods. An interval of deglaciation occurred between each period, long enough for the return and establishment of life on the newly uncovered land. During the last two decades several papers have appeared dealing with the biota of the interglacial periods, together with its significance in regard to the probable climatic conditions of those stages. Our knowledge of the types of vegetation and of the climate which existed during the interglacial epochs, especially the older ones, has been based mostly on the study of the macroscopic remains of plants and animals which lived during those periods. Deductions have also been made regarding climate and migration routes of the late interglacial periods from studies of the present distribution of biota, especially those of the relict type such as the boreal and the prairie (**35, 43, 7**).

LAGERHEIM (**23**), followed by VON POST (**36**) and others, introduced

the pollen analysis method as a means of attempting to solve the problem of interglacial changes. Since the introduction of this method very much work has been done in Europe, and in North America investigation is progressing rapidly, as shown by a recent map and bibliography published by ERDTMAN (**16**).

Through the study of the fossil pollen found at successive levels in peat deposits, the probable forest history of the area under consideration during the development of the bog may be reconstructed. Many factors must be taken into consideration before one can justly draw conclusions relative to biotic migration and climatic conditions. ERDTMAN (**13, 14**), STARK (**34**), AARIO (**1**), SEARS (**30**), and VOSS (**38**) have called the attention of workers in this field to the various sources of error.

One of the outstanding factors to be considered in the interpretation of pollen diagrams is that of pollen preservation. The conditions of hydration and acidity during the stages of development vary greatly. ERDTMAN (**14**) states: "Most of the pollen grains reaching the surface of a bog will not be preserved in a fossil state. The great supply of oxygen, the repeated wetting and drying, etc., which affect the pollen grains will hasten their destruction. The fossil pollen of the bogs, therefore, consists of those grains which were quickly carried down from the bog surface on which they landed to deeper levels with a smaller supply of oxygen and better conditions of preservation." In his work on the Canadian bogs (**15**) he again presents data showing that the height of the water table is an important factor in pollen preservation.

Account must also be taken of the variation in the quantity of pollen production by various genera found in the vicinity of bogs. Thus STARK (**34**) has shown that the amount produced by *Pinus* generally exceeds that of *Picea*. Likewise the quantity of pollen liberated by *Quercus* is less than that of *Fagus*. ERDTMAN (**15**) and AARIO (**1**), as a result of comparative studies of present forest composition and recent fossil pollen, emphasize the fact that the pollen spectrum is not always an exact picture of the forest in question.

A great variation exists in the resistance of various pollens to decay, even under conditions ideal for their preservation (**29, 15, 27**).

The question as to how far pollen travels is one that has been

considered by several workers. HESSELMAN (**21**) placed plates containing wet filter paper on ships in the Gulf of Bothnia and caught over 56,000 pollen grains of the genera *Pinus*, *Picea*, and *Betula* which had traveled more than 5.5 miles. JESSEN and RASMUSSEN (**22**) obtained in a treeless area on the Faroe Islands pollens of *Pinus*, *Alnus*, *Betula*, *Tilia*, and *Corylus* which had been carried more than 400 kilometers from their source.

In spite of its limitations, the record left by pollen is probably the most accurate one at present available, and in general, gives a rather satisfactory picture of the forests of the period.

Geology

All the bogs under consideration are located within the limits of Late Wisconsin glaciation. At the beginning of substage III (LEVERETT), the center of ice movement appears to have been in the neighborhood of Patricia in Ontario. The glacier moved southward across Lake Superior and extended west as far as central Minnesota. It also covered most of the territory north of the driftless area and reached its maximum southern extension in northeastern Illinois and northwestern Indiana. The most pronounced moraine established in northeastern Illinois during this period is the one which parallels the present shore of Lake Michigan, averages about 10 miles in width, and is known as the Valparaiso moraine. LEIGHTON (**24**) states that at the close of the Late Wisconsin sub-epoch the ice melted rapidly, causing large blocks of ice to become detached and imbedded in the Valparaiso moraine. Upon the melting of these blocks, the small lake basins in that section of the state were formed. All the Illinois bogs described in this paper developed in lakes which were apparently initiated in this way. During the recession of the Late Wisconsin ice, the waters from the melting ice cut numerous channels which later served as excellent pathways for the advancing plants and animals. Regarding the interval between the receding ice and the appearance of plants and animals, LEIGHTON (**24**) states: "Judging from the freshness of contour of the glacial moraines, from the meager amount of gullying which has taken place, except under special conditions, and from the small amount of slope wash which has gone on, it appears that the increasing warmth responsible for

the melting of the ice made possible also a rather prompt reinvasion of the plant kingdom followed no doubt also rather promptly by a return migration of the animal life."

LEVERETT's substage IV was brought about by the shifting of the center of radiation from Patricia to Keewatin in central Canada. The ice moved southward through western Minnesota, eastern North and South Dakota, and south to Des Moines, Iowa. A minor lobe crossed the Mesabi range and another extended northeastward above St. Paul to Grantsburg and Osceola, Wisconsin. At approximately the same time, the Lake Superior lobe was reaching its maximum extension when it invaded the territory north of the lake, where it probably fused with the ice from central Canada. It also invaded the land southwest of Lake Superior, northern Wisconsin and Michigan, and eastern Wisconsin as far south as Milwaukee.

During the last sub-epoch of the Wisconsin, or LEVERETT's substage V, the ice moved from central Canada covering northern Minnesota, eastern North Dakota, northeastern South Dakota, and western Minnesota.

Location of bogs

Pollen analyses were made of fourteen bogs whose location with respect to the Wisconsin drift sheets is shown in figure 1. Cedar Lake, Millburn, Wauconda, Antioch, and Volo bogs have been well described by WATERMAN (**39, 40**).

Cedar Lake bog is very immature and occupies the northwestern part of Cedar Lake, in Section 32, Township 46 N, Range 10 E, Lake County, Illinois. Near the edge of the open water the surface of the mat is quaking and the peat is over 40 feet deep. In order to reach the bottom of the lake, borings were made in the swamp zone about 100 feet from the edge of the mat.

Millburn bog is approximately 500 yards long and 300 yards wide, and is found in Section 35, Township 46 N, Range 10 E, 1 mile west of the village of Millburn, in Lake County, Illinois. The substratum is firm and covered with sphagnum, pitcher plant, and cranberry.

The bog at Wauconda is located southeast of the city of Wauconda in Section 25, Township 14 N, Range 9 E. The surface of the bog is solid with its northern half covered with tamarack and the remainder with grasses.

LAKE SUPERIOR
MINNESOTA
WISCONSIN
Driftless
Area
LAKE MICHIGAN
IOWA
MISSOURI
ILLINOIS
INDIANA
14
12
11
10
9
8
(AFTER LEVERETT, LEIGHTON, MARTIN.)
WIS. DRIFT SUBSTAGE 5
WIS. DRIFT SUBSTAGE 4
WIS. DRIFT SUBSTAGE 3
WIS. DRIFT SUBSTAGE 2
WIS. DRIFT SUBSTAGE 1
IOWAN DRIFT
UNDIFFERENTIATED DRIFT
ILLINOIAN DRIFT
KANSAN DRIFT

FIG. 1

The Antioch bog occupies a circular depression 300 yards in diameter, in Section 15, Township 46 N, Range 10 E, 3 miles southeast of Antioch, Lake County, Illinois. It is mature and bears several old trees of tamarack and yellow birch.

The Volo bog occupies an oval depression about 0.75 mile long and 0.5 mile wide, and is found on the George Sayer Farm no. 3 in Section 28, Township 45 N, Range 9 E. Open water is found in the center, surrounded by a quaking mat 75 yards wide.

The Gavin bog, so named by the writer on account of its proximity to the Gavin school, is a peat-filled lake extending north and south in Section 12, Grant Township, Lake County, Illinois. The substratum is very solid and the southern portion bears many mature tamarack trees.

The Hastings bog extends north and south in sections 22 and 27, Antioch Township, Lake County, Illinois, and is approximately 900 yards long and 200 yards wide. A small pond is found near the center and all borings were made near the north margin of the pond. Practically all the vegetation on the bog was destroyed by fire shortly before the writer visited it.

The Waupaca bog covers an area of about 60 acres and is located about 2.5 miles north of Waupaca, Wisconsin, along the tracks of the Waupaca & Green Bay Railroad. The substratum is quaking and the cover consists chiefly of sphagnum, leatherleaf, bog rosemary, Labrador tea, tamarack, and black spruce.

The Bald Eagle bog is about 0.5 mile east of Bald Eagle, Minnesota, near the boundary of Ramsey and Washington counties, in Section 1, Township 30 N, Range 22 W. It is a peat-filled lake with a non-quaking surface covered with sphagnum, alder, a few black spruce, and many large tamaracks.

The Hayward bog is located 3 miles west of the city of Hayward, Sawyer County, Wisconsin, just north of the main road running west of the city. It is bordered on the north by a low ridge, covers an area of about 200 acres, and represents a filled lake with sand forming the bottom. A narrow private road traverses the bog in a north-south direction. The bog is mature and the principal vegetation consists of tamarack, black spruce, sphagnum, pitcher plant, cranberry, Labrador tea, bog rosemary, and cassandra.

Mission Creek bog comprises an area of about 1 square mile and is located 1 mile south of Mission Creek station, along the Northern Pacific Railroad in Pine County, Minnesota. It represents a peat-filled lake. The area has been partially drained and originally was a tamarack swamp, as evidenced by the few remaining dead trees and the numerous stumps in the upper 4 feet of peat. The upper surface of the peat is firm and mostly covered with herbaceous vegetation.

Bay Lake bog is found just south of Bay Lake in Section 27, Bay Lake Township, Crow Wing County, Minnesota. It also is a peat-filled lake, having a sand and clay bottom. It is elliptical in shape, approximately 1 mile long and 0.25 mile wide, and is covered principally with sphagnum, heath shrubs, and scattered tamarack and black spruce.

The Highland bog occupies a depression between two low ridges 1 mile north of Highland, Lake County, Minnesota, along the Duluth & Iron Range Railroad. It is about 80 acres in area and consists of a filled lake, the surface of the deposit having been raised above the old water level by successive layers of sedges and sphagnum. The bog is covered with a dense growth of sphagnum, young tamarack, and black spruce.

The Coleraine bog is a small filled lake covering an area of about 12 acres, located 1 mile west of Coleraine, Itasca County, Minnesota, along the Great Northern Railroad. On the north side a steep narrow ridge separates the bog from a small lake. The bog is mature, covered mostly with sphagnum, and has a few small tamarack and black spruce trees at the west end.

Methods

The samples of peat used for pollen analysis were obtained by means of a Hiller peat augur, the construction and operation of which have been described previously (**37**). Borings were made along a line across the longest portion of the bogs and the drillings were generally 100 feet apart. The method as described by Voss (**37**) was followed in the preparation of the material for identification and counting. The identification of the pollen was carried out by means of type slides of fresh pollen and the use of Sear's drawings (**30**).

At least 150 pollen grains were counted and identified for each sample, and the pollen frequency, or number of pollen grains per square centimeter, determined. According to ERDTMAN (**12**) reliable percentages are obtained if 150 pollen grains are counted, although BOWMAN (**6**) has expressed a contrary opinion.

Results

Figures 2 to 15 show the percentages of fossil pollen and the pollen diagrams of the dominant trees, the minor ones having been omitted from the diagrams to minimize complexity. The numbers at the left of the diagrams represent the depth of the peat in feet or meters and the numbers in the horizontal scale give the percentage of tree pollen. The trees are indicated by signs, which are indexed. The stratigraphy is shown by a diagrammatic section. The type of peat designated as limnic consists of all material deposited under water. At the right of each diagram the pollen frequency curve is shown.

In all the Illinois bogs under discussion, *Abies* and *Picea* pollens reached their maximum at the bottom of the bogs and decreased nearer the surface, the decrease in some cases being gradual while in others it was abrupt. *Quercus* pollen was found in all the bottom peat and its percentage gradually increased toward the surface, the percentage remaining rather constant during the development of the major portion of the bogs. *Pinus* pollen was found at practically all levels and its percentage was also rather constant in all bogs from bottom to top. *Larix laricina* wood was encountered at the bottom of Cedar Lake, Gavin, and Millburn bogs. This wood was probably imbedded in the blocks of ice which were responsible for the original formation of the lake.

In the Waupaca (fig. 9) and the Hayward (fig. 11) bogs also, *Abies* was the dominant tree at the bottom, constituting 42 and 59 per cent respectively of the entire pollen. In both bogs *Picea* pollen was most abundant at the lowest levels, decreased toward the center, and increased nearer the surface. The *Pinus* curve of the Waupaca bog culminated at the 19 foot level and in the Hayward bog at the 8 foot level. The increase near the surface may be due to the presence

of the bog spruce, *P. mariana*, on the surrounding mature bogs. The percentage of *Quercus* pollen in the Waupaca bog was much higher than that of the Hayward bog; with an increase of *Quercus*, there was generally a decrease of *Pinus* pollen.

The pollen frequencies of the peat between the 5 and the 15 foot levels of the Mission Creek bog (fig. 12) were so low that the counts for those levels were omitted from the table and diagram. The low frequencies are perhaps due to the manner in which the peat was built up above the water level. DAVIS (**10**) emphasizes the fact that when the peat is built up above the water level, new species and more individuals appear, resulting in much dead material coming in contact with the air and the heat of the sun. This causes great loss of water and permits the growth of organisms which promote decay, thus destroying the pollen grains. The greater pollen frequency in the upper 5 feet was probably due to a change in the water content of the peat. *Abies* was the most significant tree nearest the bottom and *Pinus* and *Picea* at the top, with *Quercus* playing only a minor rôle throughout.

The pollen diagram of Bay Lake (fig. 13) is in many respects similar to that of Waupaca, the chief difference being the greater abundance of *Pinus* and *Picea* pollens and less *Quercus* pollen.

Three of the Minnesota bogs, Bald Eagle, Coleraine, and Highland, are located within substage IV of the Wisconsin epoch, and, according to LEVERETT (personal communication), are probably several thousand years younger than the other bogs in Minnesota, Wisconsin, and Illinois. WILSON (**42**) has shown that an interval existed between substages III and IV long enough for the development of a forest in eastern Wisconsin in which trees at least 80 years old were found.

Very low pollen frequencies were also obtained from the analysis of the upper 13 feet of the Bald Eagle peat, the building up process probably having taken place under conditions like those of Mission Creek.

PERCENTAGES OF FOSSIL POLLEN: WAUCONDA BOG

Depth Ft.	Abies	Larix	Picea	Pinus	Acer	Alnus	Betula	Carya	Celtis	Carpinus	Ostrya	Fraxinus	Juglans	Populus	Quercus	Salix	Tilia	Ulmus
3				13.3			3.4	3.4				.8	3.4		75.5	.8		.8
4				17.6	1.4		5.8	5.8	1.4				1.4		58.7	2.9		4.4
5				11.8	3.2	.6	3.2	9.2	1.3	1.9	1.3		.6		61.8	1.3	1.3	1.9
6		2.7		13.6			2.0	8.1					.6	.6	71.2			.6
7				19.5			1.3	2.6							76.0			.6
8				17.7				2.7							78.0			1.3
9				11.0		.6	1.3	3.2							82.0			1.9
10				13.9			.6	3.8					.6		78.0			3.1
11				13.8				4.6							81.0			.6
12				15.0			.6	6.5							74.5		1.3	1.9
13				12.6			1.9	4.6							77.0		.6	3.3
14				13.9		.6	1.3	7.3							76.0			.6
15				14.8			.6	6.4					1.2		70.5	1.2		5.1
16				8.9			1.2	9.5							71.0	.6		8.9
17				6.5			.6	5.9							76.1		1.3	9.2
18				12.2			.6	3.8							79.0	.6		3.2
19	1.2		3.1	21.3			3.1	5.6							46.0	.6	5.0	13.8
20	.6		4.2	18.2			6.0	1.8							53.2	1.2	.6	13.9
21	24.1		8.0	20.7			3.4	4.6							34.4		1.1	3.4

FIG. 2A

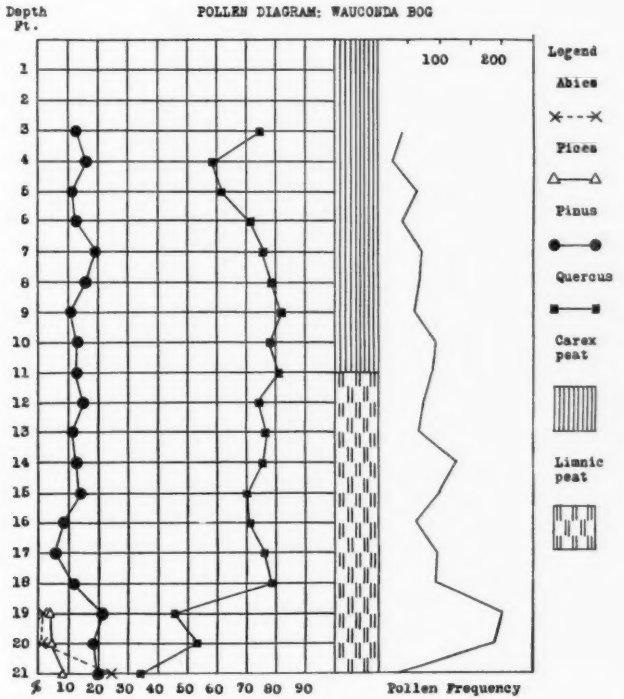

Depth
Ft.
POLLEN DIAGRAM: WAUCONDA BOG
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
%
10 20 30 40 50 60 70 80 90
100 200
Pollen Frequency
Legend
Abies
Picea
Pinus
Quercus
Carex peat
Limnic peat

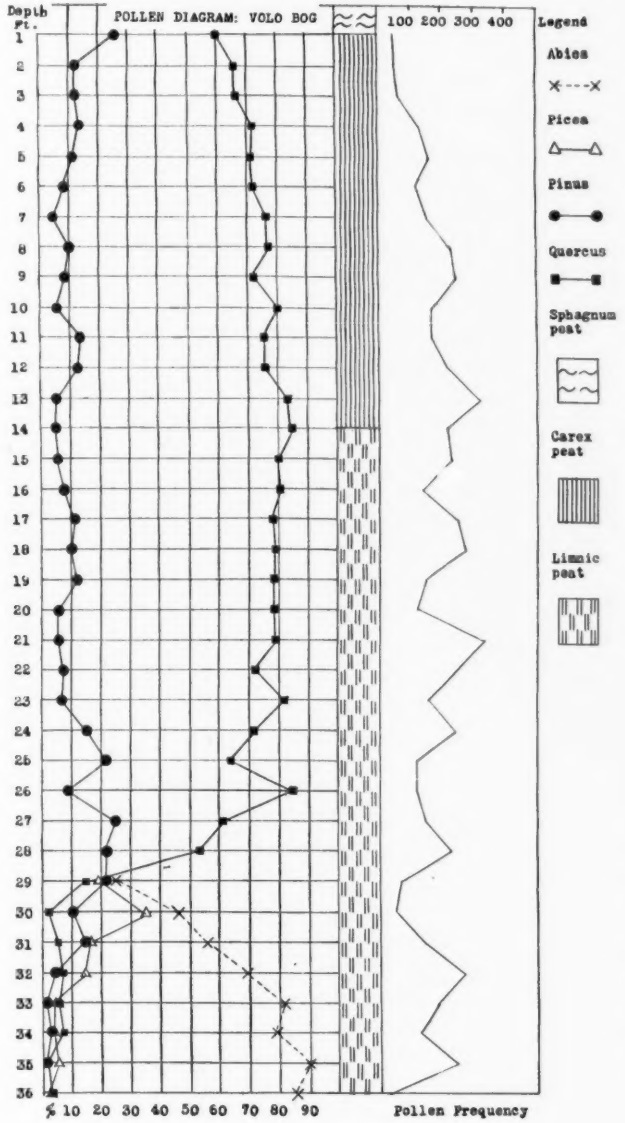
FIG. 2*B*

PERCENTAGES OF FOSSIL POLLEN

VOLO BOG

Depth Ft.	Abies	Picea	Pinus	Tsuga	Acer	Alnus	Betula	Carya	Celtis	Carpinus	Ostrya	Fraxinus	Juglans	Populus	Quercus	Salix	Tilia	Ulmus
1			26.0		3.4	.6	1.3	2.0						.6	60.0	.6		
2			12.2		1.9	1.2	3.2	3.8	1.2	.6	.6		.6	.6	66.3	1.2	2.8	3.2
3			12.9	1.9			5.8	2.6	.6			.6		1.2	66.7	1.8		.6
4			13.2	.6	.6	.6	4.2	6.0		.6	.6				72.2			.6
5			11.3	.6			2.9	7.7		2.9				1.7	71.0			1.7
6			9.8	.6			2.6	7.2		.6			.6	2.6	72.5		1.3	1.9
7			5.6		1.2		1.8	8.7		1.2			1.2		77.2			2.5
8			10.9				3.0	6.6		1.2					77.0		1.2	
9			9.3				3.7	8.1					1.2		73.9		.6	3.1
10			6.0				.6	8.7		1.3					80.5	.6	.6	1.3
11			14.0					6.6							76.5			2.6
12			13.2				.6	5.9		1.3			2.6		75.8			.6
13			6.3				1.9	5.0		.6			1.2		83.0			1.9
14			5.2	.6			2.6	5.2							85.5		.6	
15			6.1				1.2	7.2						.6	80.1			4.2
16			8.3				1.2	6.7							81.6		.6	2.6
17			11.3					5.6					.6		78.6		.6	3.1
18			10.6			.6		5.6					1.2		79.2			2.5
19			12.1				1.2	4.4					.6		78.2		.6	2.5
20			6.8				.6	4.9					.6		78.8		.6	8.0
21			6.8				3.1	5.5							79.4		1.2	3.7
22			7.6				4.5	8.3			.6				73.7		1.9	3.2
23			7.5				.6	6.2							82.3		.6	2.5
24			16.4				1.2	5.1							72.8			5.1
25			21.4				5.8	5.1							64.6		.6	1.9
26			9.5				1.3	1.3	.6						85.3		.6	.6
27			26.6				6.5	3.5							61.0			4.1
28			22.7				3.7	2.5	.6				.6		63.2		1.2	14.6
29	25.2	19.5	21.4				11.2	3.9							16.6			3.2
30	47.7	35.0	10.7				2.1	.7							2.1		.7	.7
31	56.5	16.7	16.4				4.4								5.1			2.9
32	69.4	14.9	4.8				3.2								7.1			1.3
33	81.0	4.3	1.8				5.5								6.2			1.2
34	79.5	3.8	3.1				3.1	.6							7.6			1.9
35	90.5	5.1	1.2				.6								1.9			.6
36	86.4	3.0					4.5								3.0			3.0

FIG. 3A


Depth Ft.
POLLEN DIAGRAM: VOLO BOG
100 200 300 400
Legend
Abies
Picea
Pinus
Quercus
Sphagnum peat
Carex peat
Limnic peat
1
2
3
4
5
6
7
8
9
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18
19
20
21
22
23
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25
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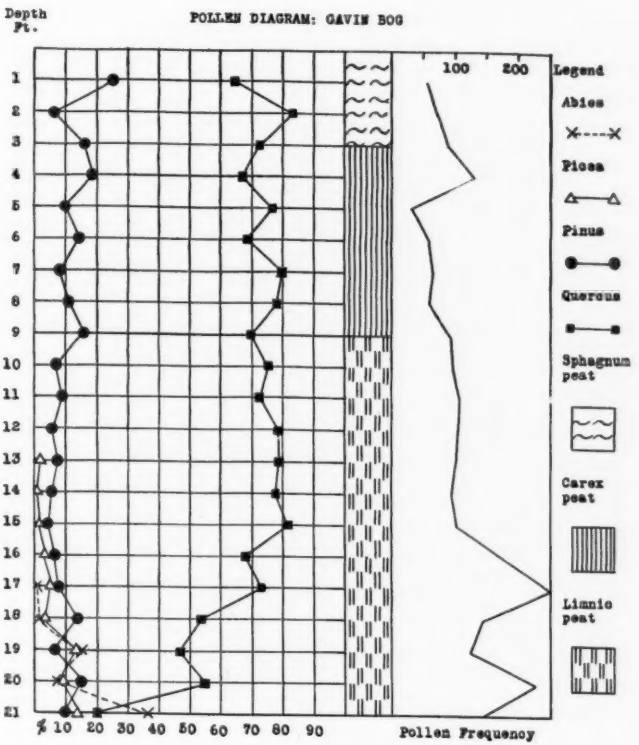
27
28
29
30
31
32
33
34
35
36
% 10 20 30 40 50 60 70 80 90
Pollen Frequency

FIG. 3*B*

PERCENTAGES OF FOSSIL POLLEN: GAVIN BOG

Depth Ft.	Abies	Picea	Pinus	Alnus	Betula	Carya	Fraxinus	Juglans	Populus	Quercus	Salix	Tilia	Ulmus
1			26.0	.6	4.0	4.6				64.0	.6		
2			7.2		3.9	4.6				83.0			1.3
3			16.5		2.6	3.9		.6		73.0	.6		2.6
4			19.3		5.1	1.9		.6		67.5	3.2		1.9
5			10.1	1.0	3.0	3.0		1.0		77.5	3.0		1.0
6		.6	14.4	.6	3.2	7.2				69.0	1.9		2.6
7			8.1		2.5	8.1				80.0			1.2
8			11.7		1.3	7.8				78.0	.6		.6
9			16.0		3.3	7.7		.6	1.3	70.0		.6	.6
10			7.0		1.2	5.7	1.2	.6		76.0	1.2	2.5	3.2
11			9.4		.6	6.9	1.8	3.1		73.5		1.8	2.5
12		1.3	5.9		1.3	5.2		1.3	.6	79.5		.6	3.9
13		.6	7.8		2.6	1.9		1.9		79.0		1.9	3.9
14			5.2		.6	3.9		.6	1.3	78.0		3.2	6.6
15		1.2	3.8		1.9	1.9				82.0		2.5	7.0
16		2.8	7.3		3.4	3.9	1.1	1.1	1.1	68.5	1.1	3.4	6.2
17	.6	4.3	8.6		1.8	.6				73.5	1.2	4.9	4.3
18	1.7	2.8	13.8		4.0	1.1				54.8	1.7	8.1	11.6
19	14.6	13.4	7.6		7.6	.6				47.9	1.2		7.0
20	7.9	8.5	14.7		3.0					54.5	2.4	4.9	3.6
21	37.5	13.2	10.0		9.4	1.8				20.6	1.8	.6	5.0

FIG. 4*A*


Depth Ft.
POLLEN DIAGRAM: GAVIN BOG
1
2
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11
12
13
14
15
16
17
18
19
20
21
% 10 20 30 40 50 60 70 80 90
100 200
Pollen Frequency
Legend
Abies
Picea
Pinus
Quercus
Sphagnum peat
Carex peat
Limnic peat

FIG. 4*B*

PERCENTAGES OF FOSSIL POLLEN

CEDAR LAKE BOG

Depth M.	Abies	Picea	Pinus	Tsuga	Acer	Alnus	Betula	Carya	Carpinus	Celtis	Juglans	Populus	Quercus	Salix	Tilia	Ulmus
.50			1.2		2.1		2.1						81.0			
.78			32.2				7.5	1.8					57.0		2.2	
1.00			23.5				2.8	1.0					71.5			.9
1.22			17.4				2.0	1.3					78.0			1.3
1.50			16.8				4.7	3.9					75.0			
1.72			13.1				2.9	2.6					78.0		.6	1.9
2.00			11.4				2.6	2.0			1.3		81.0			1.3
2.22			11.9	.6			2.6	.6			.6		82.5		.6	
2.50			16.4	.6			3.8	2.5			1.9		75.0			
2.72			14.4				3.9	1.3	.6		1.3		75.5		1.3	1.3
3.00			6.6				2.6	1.9					88.0			.6
3.22			9.8				1.3	2.6	.6				82.0		1.9	1.9
3.50			10.6				2.0	2.0					82.0		1.3	2.0
3.72			11.0	.6			1.3	2.6					82.5		.6	1.3
4.00			15.6	.6	.6		1.9	2.6					77.0		.6	.6
4.22			17.1				2.5	1.9					76.0		.6	1.2
4.50			28.7	.6			1.9	2.5	1.2				61.2		1.2	1.9
4.72			23.6	.6	1.2		1.9	3.8	.6		.6		64.0		1.2	1.9
5.00			14.0		1.9		1.3	5.9	.6				76.0			
5.22			11.8		3.4		6.4	3.4					71.0			1.7
5.50			18.7				3.4	3.4					73.0			.6
5.72			20.0				3.3	2.0					74.0		.6	
6.00			15.0				3.2	3.9					76.0		.6	1.3
6.22			13.0				4.5	1.3					78.0		1.9	.6
6.50			9.0				.6	3.8					85.0		.6	.6
6.72			7.2				2.6	3.9		1.3			82.0		1.3	1.3
7.00			20.5				2.6	5.3	.6				68.7		1.3	.6
7.22			24.5	.6			1.3	1.9		.6			68.0		1.3	1.3
7.50			15.0				1.3	3.2					76.5		.6	3.2
7.72			11.3	.7			1.4	2.8					81.5		.7	1.4
8.00			14.6				.6	1.3	1.9		.6		79.0		1.9	
8.22		.6	6.6				1.3	2.6	2.6				80.0		.6	5.3
8.50			12.2				.6	5.1	3.2				75.0		1.2	2.5
8.72		.6	13.0				1.8	2.4	1.8				75.0	1.8	1.2	1.8
9.00		.6	16.8				1.3	3.3	1.3				66.5	2.0	1.3	6.7
9.22		2.6	20.8				1.9	1.9	1.3				60.0	.6	3.2	7.2
9.50	2.0	4.0	9.2				1.3	.6	1.3				63.5	.6	.6	.6
9.72		2.1	25.2				1.4	2.8	.7				63.0		2.1	2.8
10.00	20.2	20.9	28.3			.6	4.0	.6	.6				21.0			3.3
10.22	29.7	58.0	7.6				.7		.7				3.8			
10.50	27.0	61.0	3.2				.6						7.1			.6
10.72	50.0	34.5	5.4				2.7					.6	6.7			
11.00	64.0	14.1	2.5				3.8					.6	13.6			1.2

FIG. 5*A*

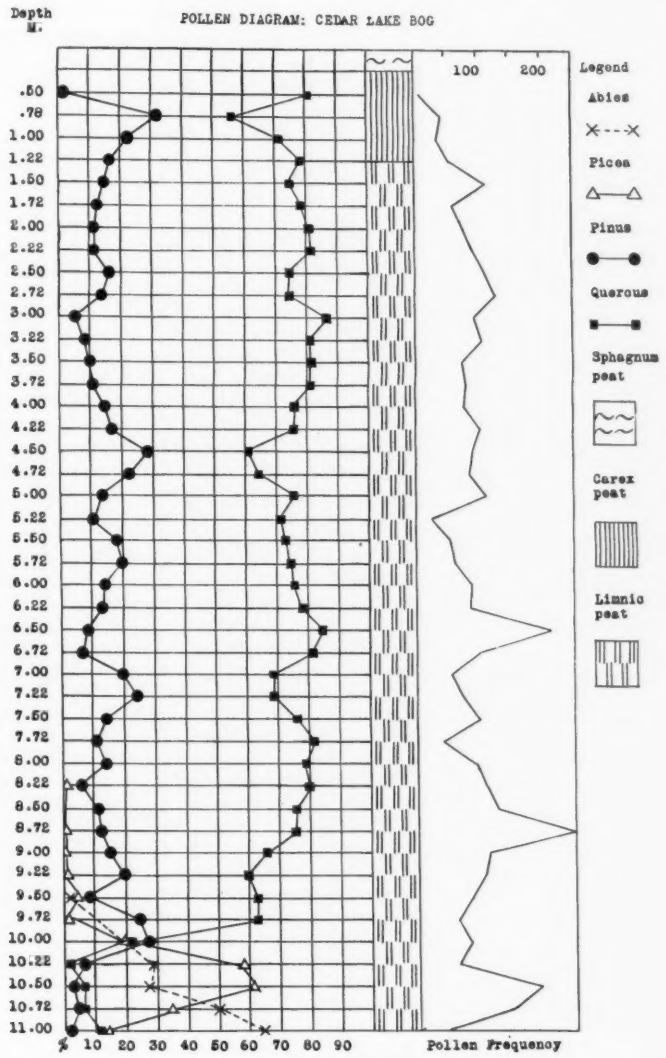

POLLEN DIAGRAM: CEDAR LAKE BOG
Depth M.
.50
.78
1.00
1.22
1.50
1.72
2.00
2.22
2.50
2.72
3.00
3.22
3.50
3.72
4.00
4.22
4.50
4.72
5.00
5.22
5.50
5.72
6.00
6.22
6.50
6.72
7.00
7.22
7.50
7.72
8.00
8.22
8.50
8.72
9.00
9.22
9.50
9.72
10.00
10.22
10.50
10.72
11.00
% 10 20 30 40 50 60 70 80 90
100 200
Pollen Frequency
Legend
Abies
Picea
Pinus
Quercus
Sphagnum peat
Carex peat
Limnic peat

FIG. 5*B*

PERCENTAGES OF FOSSIL POLLEN: ANTIOCH BOG

Depth Ft.	Abies	Picea	Pinus.	Tsuga	Alnus	Betula	Carya	Celtis	Carpinus	Corylus	Ostrya	Juglans	Quercus	Tilia	Ulmus
2			7.9			4.6	4.6						82.0		.6
3			10.6			1.9	.6						84.0		2.6
4															
5			14.6			2.4	1.2						82.0		
6			10.6			2.9	1.4						84.0	1.4	
7			11.2			2.4	7.4	3.7					75.5		
8			7.2			1.3							88.0		3.3
9			8.1	.6		.6	6.1			1.3		.6	74.0	.6	7.5
10			12.2			1.9	1.9		.6	2.5			76.0		4.5
11			4.1			.6	2.0	.6		.6		1.3	82.0	.6	7.5
12			3.8				6.3					.6	80.0	.6	8.2
13			4.0				3.3						78.0		14.2
14			2.5			1.2	3.7	.6					78.0		14.4
15			3.7			1.2	3.1						78.0	.6	13.2
16			7.0			2.5	1.2			1.2			79.0	.6	7.7
17			8.0	.6		1.8	2.4			1.2		.6	75.0		9.9
18			8.2			.6	4.4					.6	81.0	.6	4.4
19			12.1				3.2						74.5	1.9	8.3
20		.6	8.7	.6		2.0	2.6			.6		1.3	68.0	2.0	12.7
21	1.3	1.3	16.4			3.2	1.3	1.3		1.3	2.6	1.3	47.0	1.3	21.5
22	30.5	18.4	9.5		.6	8.3	.6						17.2		14.6

FIG. 6A

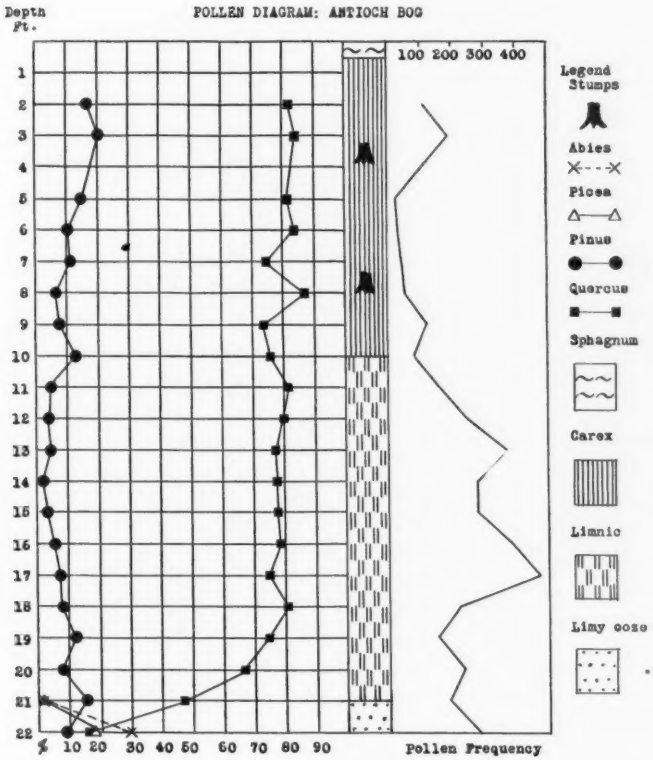

Depth
Ft.
POLLEN DIAGRAM: ANTIOCH BOG
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
%
10 20 30 40 50 60 70 80 90
100 200 300 400
Pollen Frequency
Legend
Stumps
Abies
Picea
Pinus
Quercus
Sphagnum
Carex
Limnic
Limy ooze

FIG. 6B

PERCENTAGES OF FOSSIL POLLEN

MILLBURN BOG

Depth M.	Abies	Picea	Pinus	Tsuga	Betula	Carya	Carpinus	Juglans	Quercus	Salix	Tilia	Ulmus
.35			13.6		11.0	5.2	.6		61.7	7.1		.6
.72			24.7		4.3	1.4			64.1	5.1		
1.00			18.0	.81	2.4	1.6		.8	71.5	3.2		1.6
1.72			6.4		3.2	2.5	.6		83.2	2.5		1.2
2.00			8.5	.6	.6	3.2	.6		80.3	5.2		.6
2.72			7.7	.6	3.8	4.5		.6	78.0	2.5		1.9
3.00			15.3	1.8	1.2	8.1	1.2		68.5	1.8	.6	1.2
3.72			11.7		3.1	9.2	1.2		69.8	1.2		3.7
4.00			12.4		3.9	6.5	1.3		74.6	.6		.6
4.72			14.2		2.5	3.2			77.2			2.5
5.00			5.8	1.2	2.5	3.8			81.0	1.9		3.2
5.72		.6	8.1		.6	3.4	.6		83.8	2.7		
6.00		.8	13.4		2.6	7.1			74.0		.8	.8
6.72			11.3		2.0	3.3			81.3		.6	1.3
7.00			11.6		1.9	3.9			78.0		.6	3.9
8.22			5.8		1.2	1.9			85.5	.6	.6	3.8
8.36			8.4		3.2	1.3	.6		78.4	.6	.6	6.5
8.50			19.4		.6	1.2	.6		71.0		3.1	3.1
9.47	2.8	5.4	20.3		8.1	1.1	.5		52.5		.5	8.6
9.75	17.2	54.9	14.6		6.3	.6			6.3			
10.47	36.6	18.7	6.6		4.6	4.0			22.0	2.6		4.6
10.61	74.8	18.7							6.6			

FIG. 7A

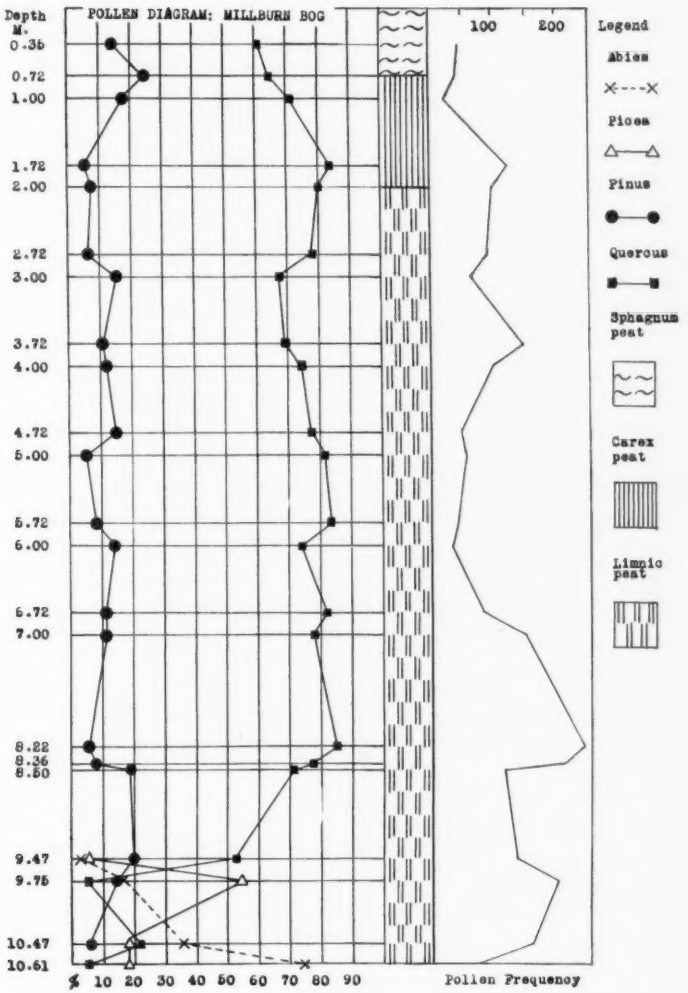

POLLEN DIAGRAM: MILLBURN BOG
Depth M.
0.36
0.72
1.00
1.72
2.00
2.72
3.00
3.72
4.00
4.72
5.00
5.72
6.00
6.72
7.00
8.22
8.36
8.50
9.47
9.75
10.47
10.61
% 10 20 30 40 50 60 70 80 90
100 200
Pollen Frequency
Legend
Abies
Picea
Pinus
Quercus
Sphagnum peat
Carex peat
Limnic peat

FIG. 7*B*

PERCENTAGES OF FOSSIL POLLEN

HASTINGS BOG

Depth Ft.	Abies	Picea	Pinus	Alnus	Betula	Carya	Juglans	Populus	Quercus	Salix	Tilia	Ulmus
1			13.6		1.6	4.8	.8		75.0	2.4		1.6
2			11.3		.8	5.6	.8		88.0			
3			12.2		3.8	1.9			81.2			.6
4			5.9		1.4	4.4			88.0			
5			12.1		1.9	2.5			82.0			1.2
6			10.5		2.5	2.5			82.0	1.2		1.2
7			12.7		.7	3.7			81.2	.7	.7	
8			12.8	.9	1.9	3.8	1.9		77.0	.9		1.2
9			6.5			3.9	1.3		87.0		.6	
10			6.8		2.2	3.1	.7	.7	87.0	2.2		.7
11			16.8		2.6	1.7			78.0	.8		
12			13.7		3.9	2.9	.9		76.5	.9		.9
13			8.1		4.0	1.6			87.0	1.6	.8	
14			10.2		1.7	.8			86.5	.8		1.2
15			10.0		1.2	1.6			86.2			
16			11.4		2.0	1.3			84.5			.6
17			5.5		.7	3.1	.7		87.1	.7	.7	.7
18			8.2	.6	1.9	6.9	.6		79.5			1.9
19					.6	3.7			88.0		1.8	5.5
20			3.9		.6	2.6			89.2		1.3	1.9
21		.6	16.2		1.2	1.8			75.0	.6	1.8	2.5
22			13.5		3.2	3.2			75.0			4.5
23		5.1	15.9		3.8	3.1			64.0		5.7	12.1
24		2.4	17.5		3.6	4.2			56.2	.6	1.8	13.3
25		1.2	15.9		5.7	1.9			62.3	1.9		10.8
26	8.7	11.4	17.5		19.0	.6			24.6	1.9	1.9	13.9
27	39.0	13.7	20.2		9.1				13.7			4.5
28	72.1	13.2	5.9		1.9				5.9			.6
29	73.5	9.2			2.6				13.2			1.3

FIG. 8*A*

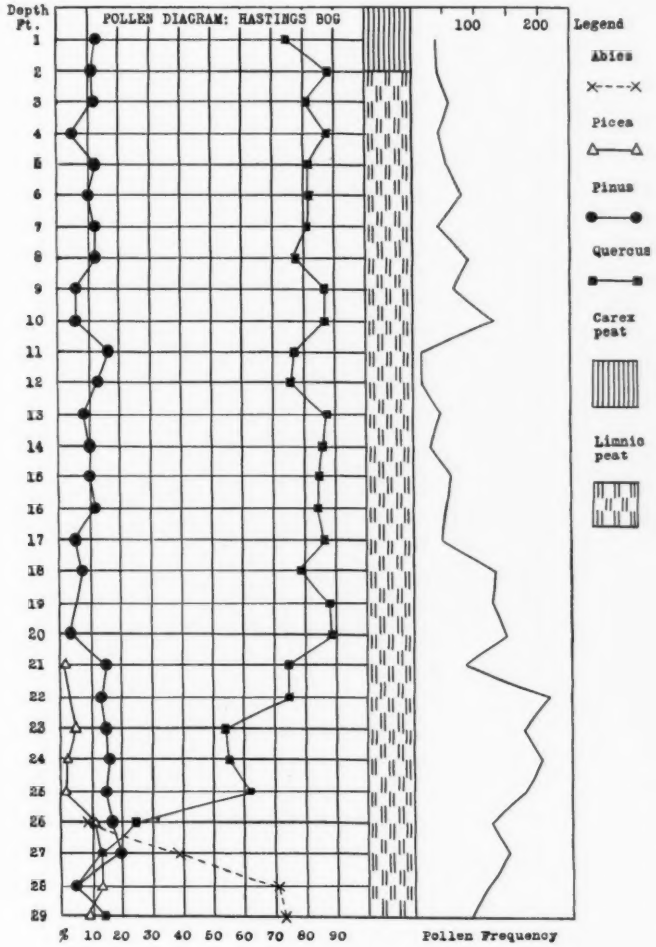

Depth Ft.
POLLEN DIAGRAM: HASTINGS BOG
100
200
Legend
Abies
Picea
Pinus
Quercus
Carex peat
Limnic peat
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
% 10 20 30 40 50 60 70 80 90
Pollen Frequency

FIG. 8*B*

PERCENTAGES OF FOSSIL POLLEN

WAUPACA BOG

Depth Ft.	Abies	Picea	Pinus	Tsuga	Alnus	Betula	Carya	Carpinus	Corylus	Ostrya	Fagus	Juglans	Quercus	Tilia	Ulmus
1		19.3	42.5	1.3	3.9	5.3		2.6	.6			1.3	21.9	.6	
2		17.8	41.5	4.7	3.5	7.1	.5	2.6		.6		1.1	19.6		1.1
3		11.0	33.5	4.0	5.8	4.6	1.1	2.3	.5	1.1		.5	34.5		.5
4		4.6	37.0	3.9	7.2	3.9	1.3	1.9		1.3		1.9	36.0		
5		6.0	37.0	2.4	6.0	3.0	.6	2.4			1.2	1.8	39.0	.6	
6		3.8	32.5	1.9	7.6	2.5		1.2			1.9	.6	48.0		
7		5.8	34.0	2.3	7.5	2.3		1.7			1.7	2.3	42.0		
8		3.2	26.2	1.2	5.7	3.2	.6	3.2			.6	2.5	53.0		
9		2.0	26.0		6.0	2.6	.6	2.5			.6		57.0		2.0
10		3.0	33.4		3.0	2.4	1.2	1.2	.6		1.2	1.2	52.5		
11		2.6	32.5		3.2	3.2		1.9	.6	.6	3.9	1.9	46.0	.6	2.6
12		1.7	38.7		4.7	1.1		2.3			2.3	.6	42.2	.6	5.3
13		1.2	49.0	1.2	2.4	1.2		.6			1.8		38.0		4.8
14		3.5	43.5		1.7	2.3	.5	.5		1.1	1.7		40.0		4.8
15		1.9	43.0		2.6	.6	.6				1.9	1.9	41.5	.6	5.1
16		3.7	53.0		3.1	1.8					2.5	.6	28.5	.6	6.2
17		2.0	62.8		5.4	2.7	.6	1.3			.6		20.3	.6	3.3
18		7.8	64.3		1.9	1.2	.6				1.2	.6	16.1		5.8
19		3.9	68.0		3.9	1.3	.6						17.0		5.2
20		1.7	66.0		5.9	1.1	1.7	1.1					18.2	.5	3.5
21	4.3	36.2	38.5	.6	2.6	3.1		1.2					11.8	.6	.6
22	32.5	45.8	12.1			1.2						.6	7.0	.6	
23	42.7	42.0	11.6			.6							2.6		

FIG. 9A

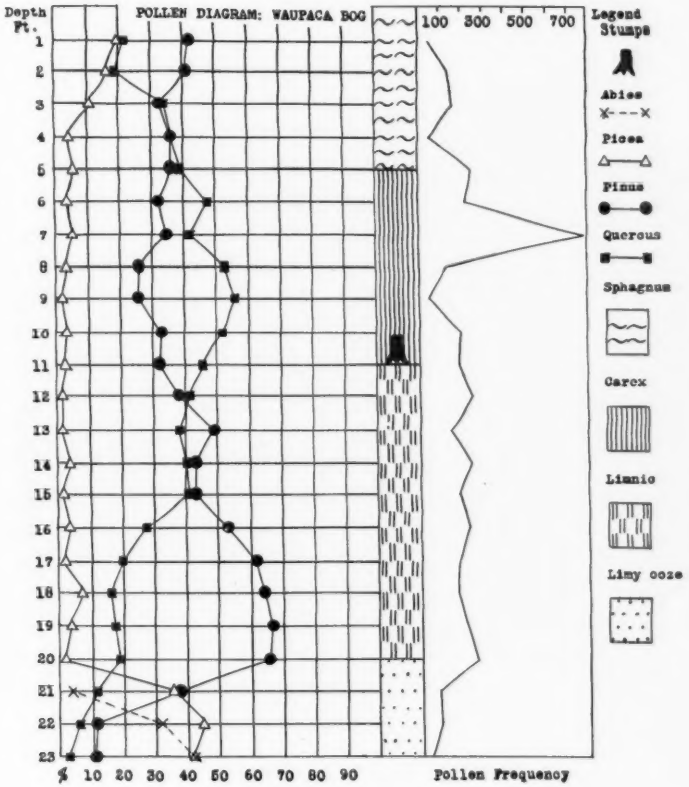

Depth Ft.
POLLEN DIAGRAM: WAUPACA BOG
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
%
10 20 30 40 50 60 70 80 90
100 300 500 700
Pollen Frequency
Legend
Stumps
Abies
Picea
Pinus
Quercus
Sphagnum
Carex
Limnic
Limy ooze

FIG. 9*B*

PERCENTAGES OF FOSSIL POLLEN

BALD EAGLE BOG

Depth Ft.	Abies	Picea	Pinus	Alnus	Betula	Corylus	Populus	Quercus	Salix	Tilia	Ulmus
13		12.4	49.3	.6	2.5			26.2	1.3		5.9
14	.6	12.9	51.5	.6	4.5	.6	1.9	15.4	1.9	3.8	5.8
15	1.8	22.0	51.2	3.5	2.4			9.7	.6	1.2	7.9
16	9.6	48.0	25.5		10.9			3.8			1.9
17	83.5	8.5	2.6		2.6			1.9			.6
18	79.5	15.7	3.9		.6						
19	81.0	15.0	1.9		1.3			.6			
20	87.5	9.4	.6		1.2						

FIG. 10*A*

POLLEN DIAGRAM: HAYWARD BOG

Depth Ft.	Abies	Picea		Tsuga	Betula	Carya	Ostrya	Quercus	Salix	Tilia	Ulmus
1		25.5	62.5		7.5			4.3			
2		25.9	66.0		2.4			3.7	.6		1.2
3		10.2	76.0		2.5			6.9	3.1		1.2
4		3.6	77.0		3.6	.6		12.2	.6		2.4
5		3.0	82.0		1.8			12.0			1.2
6		3.2	77.0	.6	1.2	.6		13.5		1.2	1.9
7	.6	2.5	78.0		1.9		.6	12.0	.6	1.2	1.9
8	2.4	8.5	82.0		1.8		.6	1.2		1.8	1.8
9	3.8	20.5	67.0					5.1	.6	1.2	1.2
10	59.0	26.2	3.6		1.7			4.8		1.7	2.4

FIG. 11*A*

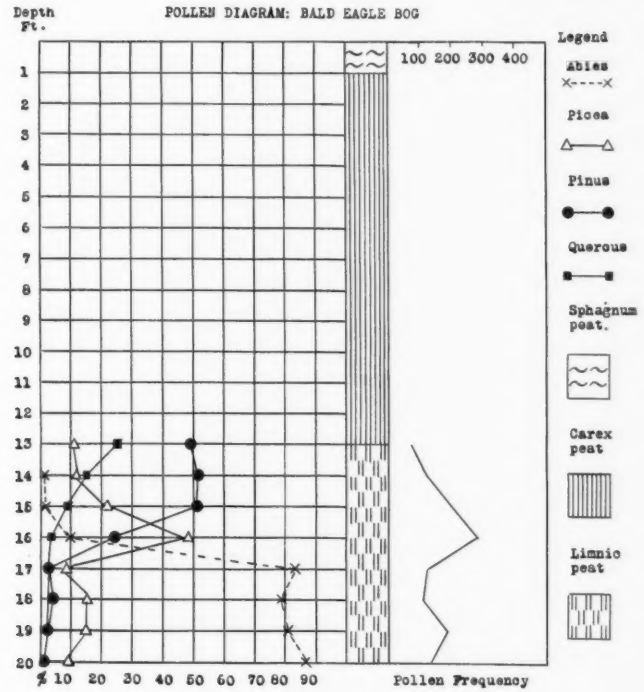


FIG. 10*B*

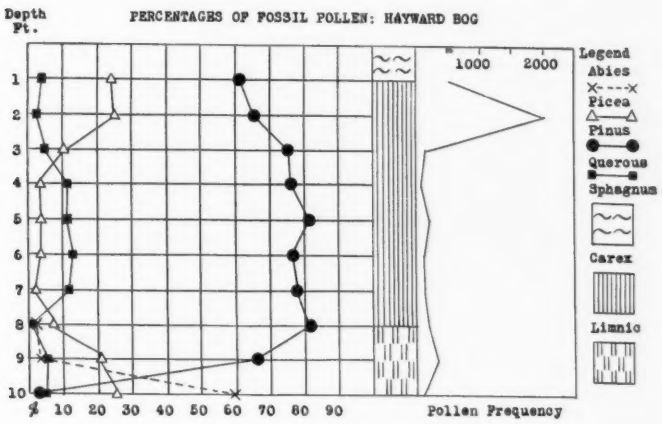


FIG. 11*B*

PERCENTAGES OF FOSSIL POLLEN

MISSION CREEK BOG

Depth Ft.	Abies	Picea	Pinus	Alnus	Betula	Fraxinus	Populus	Quercus	Salix	Ulmus
1		19.9	71.2		1.9			6.4	.6	
2		22.7	72.0		3.2			1.3		.6
3		28.3	64.5	.6	3.8			2.8		
4		33.0	62.0	.6	1.9			1.9		.6
5	1.2	36.2	54.0	.6	1.9			5.1	.6	
15	3.2	12.4	55.5	3.2	13.1	.6		1.3	.6	3.9
16	13.6	23.0	47.2	.6	6.8		.6	4.9		3.1
17	81.5	10.4	4.5		1.3		1.3	1.3		
18	94.0	4.4	.6					.6		

FIG. 12*A*

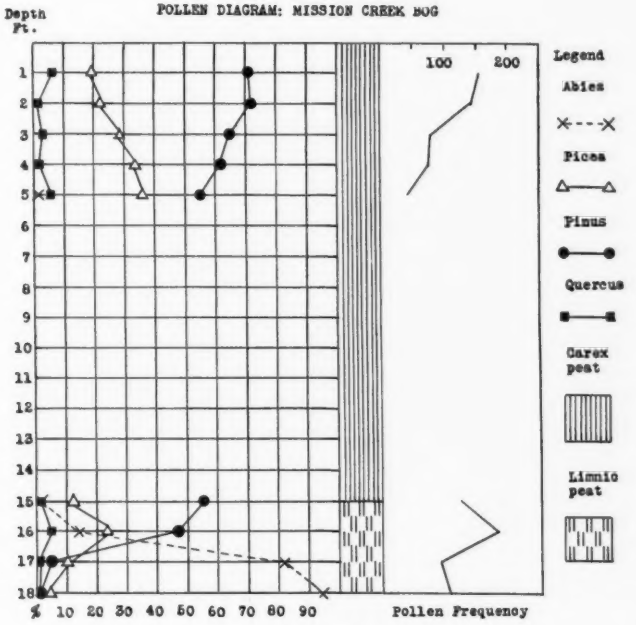


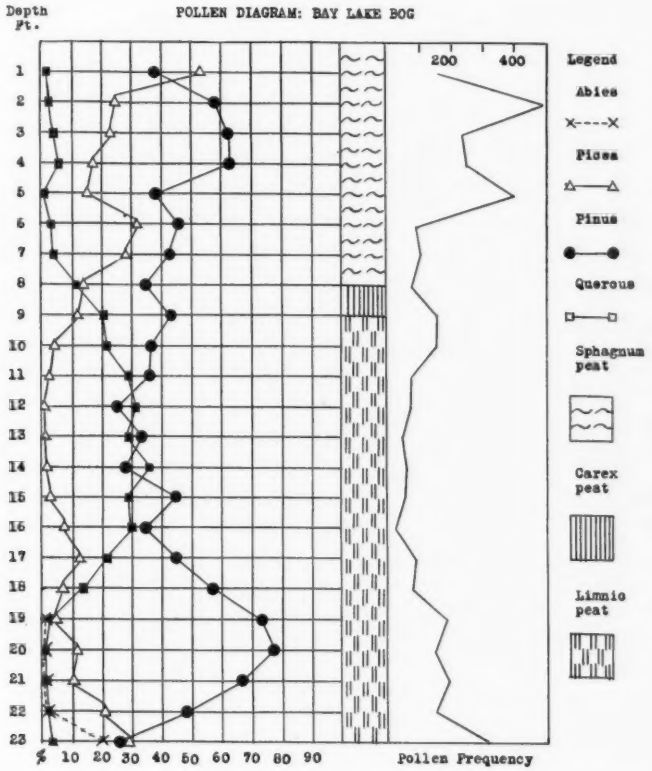
FIG. 12*B*

313635

PERCENTAGES OF FOSSIL POLLEN: BAY LAKE BOG

Depth Ft.	Abies	Picea	Pinus	Acer	Alnus	Betula	Carya	Corylus	Ostrya	Populus	Quercus	Salix	Tilia	Ulmus
1		53.2	38.2		.6	5.5					1.8	.6		
2	.6	24.8	58.3		.6	11.4					2.5		1.2	
3	1.2	23.4	62.5		1.2	6.9					3.8		.6	
4	1.2	17.7	63.0		1.2	9.7					5.4		1.8	
5		16.5	38.6		3.6	38.6					1.8	1.8		
6	3.2	31.7	46.6		.6	11.1					3.8	1.9	.6	
7	1.9	28.8	43.0		1.2	19.8					4.4	.6		
8	.6	13.5	35.5		7.1	30.3					12.5		.6	
9	.6	11.5	43.0		2.4	14.6					20.5	2.4	3.0	1.8
10	.6	4.6	36.3		1.9	20.4					21.7	6.6	3.9	3.9
11		3.1	36.9		7.0	13.4					29.3	9.5		.6
12	.6	.6	25.8		9.4	18.8	.6		1.2		31.4	10.0	.6	.6
13		1.2	33.3		7.6	14.7					29.5	12.8		.6
14		1.9	28.4		5.2	18.5					36.4	7.9		1.3
15		3.1	44.5		3.1	6.3					29.0	9.4	.6	3.7
16	.8	8.6	34.5		4.3	9.5					30.0	8.6	.8	2.5
17		12.5	44.2		1.2	13.1	.6			.6	21.2	6.2		
18		7.9	57.8		1.9	11.8				.6	14.8	3.2		2.6
19	.6	4.3	73.5		2.5	5.6			1.8		3.7	4.3		3.1
20	.6	12.8	77.3		1.8	2.4			1.2	1.2	1.2	.6		.6
21	.6	10.2	66.0		3.2	10.2		3.2		1.2	1.2			3.8
22	2.4	21.5	48.5		2.9	16.1		1.2		3.6	1.8			1.8
23	19.9	28.4	17.0	1.7	3.9	20.4		2.2		2.2	2.8	.5		.5

FIG. 13*A*


Depth Ft.
POLLEN DIAGRAM: BAY LAKE BOG
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19
20
21
22
23
%
10 20 30 40 50 60 70 80 90
200
400
Pollen Frequency
Legend
Abies
Picea
Pinus
Quercus
Sphagnum peat
Carex peat
Limnic peat

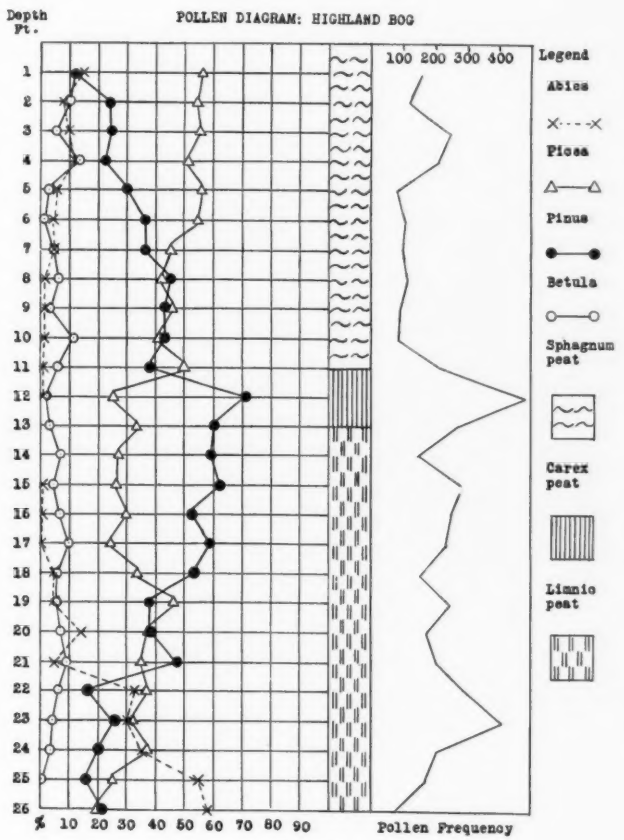
FIG. 13*B*

PERCENTAGES OF FOSSIL POLLEN

HIGHLAND BOG

Depth Ft.	Abies	Picea	Pinus	Alnus	Betula	Quercus	Salix	Ulmus
1	14.8	57.0	12.2	2.3	12.2	.6		
2	8.9	54.2	23.0	2.9	10.0	.5		
3	10.3	55.3	24.5	2.5	6.4	.6		
4	12.6	61.0	22.7		13.1	.6		
5	6.5	56.7	30.0	2.6	3.9			
6	5.0	54.0	37.0		2.5	.6	.6	
7	5.6	45.7	37.6	1.8	5.0	2.5	1.2	
8	1.2	42.5	45.0	1.9	7.6	1.9		
9	1.9	47.7	44.5	1.2	3.1		.6	.6
10	1.3	41.0	43.5	2.6	11.0	.6		
11	1.2	50.0	38.5	2.5	7.6			
12	.6	26.0	71.5		1.3	.6		
13		33.5	60.5	1.2	3.8	1.9		
14		28.2	59.0	3.1	8.1	.6		.6
15	1.2	27.0	62.0	3.0	4.3	1.2	.6	.6
16	1.1	30.3	53.7	2.2	8.5	.5	.5	2.8
17	.6	24.0	59.2	3.6	10.8	1.2	.6	
18	5.6	33.5	53.0	.6	6.8		.6	
19	5.1	47.0	38.0		6.3	3.2		
20	14.2	38.7	38.7		8.4			
21	5.5	35.0	48.0		9.8	1.2		.6
22	33.6	37.0	17.0		7.0	1.7	2.9	.6
23	30.2	32.5	26.6		4.8	1.2	2.4	2.4
24	35.0	37.0	20.4		4.7	2.7		
25	55.0	25.7	17.7		.6	.6		
26	58.5	19.4	21.3			.6		

FIG. 14*A*


Depth Ft.
POLLEN DIAGRAM: HIGHLAND BOG
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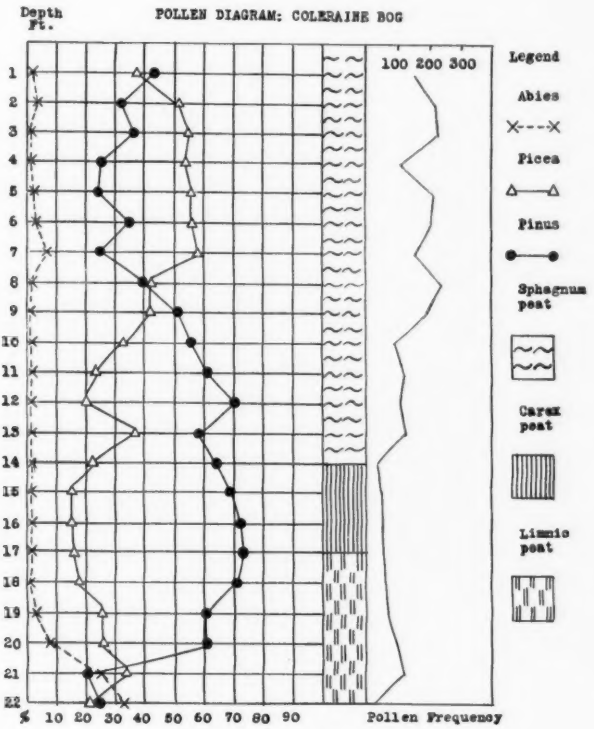
23
24
25
26
% 10 20 30 40 50 60 70 80 90
100 200 300 400
Pollen Frequency
Legend
Abies
Picea
Pinus
Betula
Sphagnum peat
Carex peat
Limnic peat

FIG. 14*B*

PERCENTAGES OF FOSSIL POLLEN: COLERAINE BOG

Depth Ft	Abies	Picea	Pinus	Alnus	Betula	Corylus	Carpinus	Ostrya	Juglans	Populus	Quercus	Salix	Tilia	Ulmus
1	1.2	38.5	43.5	3.7	7.5						1.8	.6		.6
2	4.4	51.8	32.5	2.5	3.8		2.5				1.2			.6
3	1.3	54.5	37.5	3.4	2.0						.6			
4	1.8	53.0	25.8	6.6	6.6		3.1				3.6			
5	3.4	56.0	23.1	3.4	11.0		1.1				1.1		.5	.5
6	3.1	58.8	34.0		1.8						1.8			
7	8.2	59.9	25.5	1.2	3.8		.6				.6			
8	1.9	42.5	39.9	3.9	7.3						3.9			
9	.6	42.2	51.0	1.8	2.4						1.8			
10	1.3	32.6	57.1		2.6						4.0	2.0		
11	1.9	23.0	61.0	1.9	2.5		1.2				8.3			
12	.6	20.4	70.0	1.9	4.4						2.5			
13	.6	37.5	58.0		2.0						1.3			
14	.6	22.4	64.0	.6	2.5		.6				3.8	3.8		
15	.7	15.6	69.0		1.4		.7	1.4	.7		5.9	3.7		.7
16	.6	15.2	72.0		.6	.6	1.2		.6		9.1			
17	.6	16.6	73.0		2.5						2.5	3.8		.6
18	.6	18.0	71.5		3.2						2.5	3.2		.6
19	3.7	26.0	60.0		4.9		1.2	.6			1.8			1.2
20	8.5	26.0	61.0		.6		1.3				1.3			1.3
21	25.6	33.5	20.7		12.8					.6	2.4	1.8		2.4
22	32.7	21.0	23.6	1.3	9.8						1.9	7.2		1.9

FIG. 15.4


Depth Ft.
POLLEN DIAGRAM: COLERAINE BOG
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21
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% 10 20 30 40 50 60 70 80 90
100 200 300
Pollen Frequency
Legend
Abies
Picea
Pinus
Sphagnum peat
Carex peat
Limnic peat

FIG. 15*B*

The pollen diagrams of the two northernmost bogs, Coleraine (fig. 15) and Highland (fig. 14), reveal the predominance of *Abies* while the lowest levels were being deposited, and its pollen is found in lower percentages at practically all levels upward. The *Pinus* curve culminates near the center and decreases toward the surface, while the *Picea* curve remains rather constant from the bottom to the center of the bogs and then gradually increases. *Quercus*, in contrast to the older and more southern bogs, was always less than 10 per cent at all levels in both bogs.

Conclusions

When the Late Wisconsin ice sheet reached its maximum extension in Illinois, the conditions controlling the flora of the region south of the ice edge were probably as pictured by TRANSEAU (**35**), WOODARD (**43**), and others. South of the Valparaiso moraine the country was evidently comparatively flat and dissected by several pre-Late Wisconsin streams. While the ice sheet remained stationary and formed the Valparaiso moraine, most of Illinois, because of climatic conditions, was occupied by tundra as far south as the southern part of Williamson County. East of Illinois the tundra, owing to differences in topography, gradually became narrower whereas west of Illinois it was probably much wider.

Immediately below the tundra, between the Appalachian and Ozark mountains, where temperate conditions and abundant rainfall prevailed, there was probably a mixture of conifer and deciduous forests. These forests, like all other biota, had previously been forced to migrate southward by the advancing glacier. Probably a definite conifer belt existed next to the tundra, which, according to ADAMS (**5**), may have reached the latitude of the Ohio valley, with extensions farther south at higher elevations.

In the southeast the edaphic and climatic conditions for the support of a deciduous forest were ideal (**4**), and as ADAMS (**5**) states: "This area has been important not only as a region of preservation, but also as a center of origin. Here is found the best development of the deciduous forest . . . . of North America."

With the decline of the Late Wisconsin ice sheet, many modifications in topography were brought about by the waters from the melt-

ing ice. New drainage channels were formed and others filled with drift. Many depressions were also formed which later aided in the dissemination of plant life. As the Late Wisconsin ice receded, it deposited drift which was far more hilly than that of the Early Wisconsin, and this later served as an excellent environment for the invading forests.

With an amelioration of climate, there naturally followed a slow migration of plant and animal life, the rate and type of succession depending upon climatic, edaphic, and topographic conditions. The edaphic effect has been emphasized by FULLER (**17**), WOODARD (**43**), DE FOREST (**11**), WILDE (**41**), and the topographic by FULLER (**18**). The tundra plants closely followed the edge of the retreating ice, and as their remains accumulated and became part of the soil, they paved the way for the succeeding biota.

Several drainage channels, the most important being the Mississippi, Rock, Illinois, and Wabash rivers, served as pathways for the invading forests from the south. All pollen diagrams indicate that the conifers *Abies* and *Picea* were the first dominant trees to appear on the newly uncovered land. As the climate became warmer and edaphic conditions changed, the oaks, maples, etc., gradually invaded and superseded the conifers on the uplands (**43, 8**). Along the streams the pioneers were probably similar to those under like conditions today (**9**).

The results of the pollen analyses of the eleven bogs found within the limits of substage III of the Wisconsin epoch agree in many respects with those of SEARS (**31, 32**) and AUER (**2**). Reporting on his study of 28 bogs, AUER states: "In the bottom layer of peat bogs in southeastern Canada, *Picea* and *Abies* pollen appear in abundance, but their curve, a little higher up, rapidly drops to a minimum, when the pollen amounts of the hardwood reach their highest value. In the surface parts the pollen amount of spruce trees again increases, whereas that of hardwood is decreasing."

The northern bogs, Coleraine and Highland, which are younger than those of substage III of the Wisconsin, show that the type of vegetation has remained practically the same throughout their development. This may be attributed chiefly to climatic conditions.

The pollen diagrams of the bogs found upon the drift of substage

III indicate that climatic conditions remained very uniform during the period represented by the upper two-thirds of the diagrams. Likewise no indications of climatic fluctuations are seen in the diagrams of the substage IV bogs. These studies do not show evidence of such climatic fluctuations as those found in Europe and designated in the Blytt-Sernander hypothesis (**44**). They also do not seem to afford any data that would support the hypothesis of SEARS (**33**) that five or six variations of climate have occurred in postglacial times.

Summary

1. Taking into consideration all the limitations of pollen analysis, the fossil pollen counts of fourteen bogs in Illinois, Wisconsin, and Minnesota show the succession of the forests during their entire development.

2. Eleven bogs are found within the limits of substage III of the Wisconsin epoch, and three within the limits of substage IV.

3. *Abies* and *Picea* pollen were the predominant ones at the lowest levels in all bogs.

4. Dryness and decay of peat often renders it unfit for pollen analysis.

5. The bogs of substage III reveal a succession from *Abies-Picea* forests to deciduous ones, the oaks being the predominant trees of the latter. The change from *Abies-Picea* to deciduous forests is generally abrupt, and if the thickness of peat is considered an indicator of age, the *Abies-Picea* period, especially in the southern bogs, was shorter than the deciduous period. *Quercus* pollen was more abundant in the southern bogs.

6. The younger northern bogs belonging to substage IV show that the conifers have been the significant trees throughout their history.

7. Climatic conditions remained very uniform throughout the period represented by the upper two-thirds of the pollen diagrams.

8. The results do not correlate with the Blytt-Sernander hypothesis.

Grateful acknowledgments are due to Dr. GEORGE D. FULLER of the University of Chicago for his careful supervision and thoughtful criticism during the course of this study; to Dr. GUNNAR ERDTMAN

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LITERATURE CITED

1. AARIO, L., Pflanzentopographische und paläogeographische Mooruntersuchungen in N-Satakunta. Communicationes Inst. Forestalis Fenniae **17**:1–189. 1932.
2. AUER, V., Some problems of peat investigation in Canada. Canadian Geol. Survey, Summary Report. Part C. 1927.
3. ADAMS, C. C., Post-glacial origin and migration of the life of northeastern United States. Jour. Geography **1**:303–310; 352–357. 1902.
4. ———, Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull. **3**:115–132. 1902.
5. ———, The post-glacial dispersal of the North American biota. Biol. Bull. **9**:52–70. 1905.
6. BOWMAN, P. W., Study of a peat bog near the Matamek River, Canada, by the method of pollen analysis. Ecology **12**:694–708. 1931.
7. BRAUN, E. L., Glacial and post-glacial plant migration indicated by relic colonies of southern Ohio. Ecology **9**:284–302. 1928.
8. COOPER, W. S., and FOOT, H., Reconstruction of a late-Pleistocene biotic community in Minneapolis, Minn. Ecology **13**:63–72. 1932.
9. COWLES, H. C., The plant societies of Chicago and vicinity. Geog. Soc. Chicago. Bull. 2. 1901.
10. DAVIS, C. A., Origin and distribution of peat in Michigan. Rept. Mich. State Bd. Geol. Survey. 1907.
11. DE FOREST, H., The plant ecology of the Rock River woodlands of Ogle County, Illinois. Trans. Ill. State Acad. Science **14**:152–183. 1921.
12. ERDTMAN, G., Pollenanalytische Untersuchungen von Torfmooren und marinen Sedimenten in Südwestschweden. Arkiv. Botanik **17**:No. 10. 1921.
13. ——— Pollen-statistics: a new research method in palaeo-ecology. Science **73**:399–401. 1931.
14. ———, The boreal hazel forests and the theory of pollen statistics. Jour. Ecology **19**:158–163. 1931.

15. ERDTMAN, G., Worpswede-Wabamum. Ein pollenstatistisches Menetekel. Sonderabdruck aus Abh. Nat. Ver. Bremen, Bd. 28. Sonderheft. 1931.
16. ———, Literature on pollen-statistics and related topics published 1930 and 1931. Geol. Fören. Föhr. Stockholm **54**:395–418. 1932.
17. FULLER, G. D., Soil as a limiting factor of forests in LaSalle County, Illinois. Trans. Ill. State Acad. Science **12**:99–103. 1919.
18. ———, Topographic relief as a factor in plant succession. Trans. Ill. State Acad. Science **13**:243–247. 1920.
19. GLEASON, H. A., The vegetational history of the middle west. Ann. Assoc. Amer. Geographers **12**:39–85. 1923.
20. HARSHBERGER, J. W., An ecologic study of the flora of mountainous North Carolina. BOT. GAZ. **36**:241–258. 1903.
21. HESSELMAN, H., Om pollenregn pa hafvet och fjärrtransport af barrtraedspollen. Geol. Fören. Stockholm. 1919.
22. JESSEN, K., and RASMUSSEN, R., Et profil gennem en Torvemose paa Faeroerne. Danm. Geol. Unders. IV. R. Bd. 1. 1922.
23. LAGERHEIM, G., and WITTE, H., Stratiotes aloides L. funnen i Sveriges postglaciala aflagringar. Geol. Fören Förh. Bd. 27. 1905.
24. LEIGHTON, M. M., The glacial history of the Elgin region. Trans. Ill. State Acad. Science **17**:65–71. 1924.
25. LEVERETT, F., Moraines and shore lines of the Lake Superior region. U.S. Geol. Survey, Prof. Paper 154A. 1929.
26. LEVERETT, F., and SARDESON, F. W., Quaternary geology of Minnesota and parts of adjacent states. U.S. Geol. Survey. Prof. Paper 161. 1932.
27. MÄLSTROM, C., Degerö Stormyr en botanisk, hydrologisk och utvecklingshistorisk undersokning över ett nordsvenskt myrkomplex. Meddel. fran Statens Skogsförsöksanstalt. 1923.
28. MARTIN, L. The physical geography of Wisconsin. Wis. Geol. & Nat. Hist. Survey. Bull. 36 ed. Ser. No. 4. 1916.
29. RUDOLPH, K., and FIRBAS, F., Pollenanalytische Untersuchungen böhmischer Moore. Ber. Deutsch. Bot. Ges. **40**:393–405. 1922.
30. SEARS, P. B., Common fossil pollen of the Erie basin. BOT. GAZ. **89**:95–106. 1930.
31. ———, A record of post-glacial climate in northern Ohio. Ohio Jour. Science **30**:205–217. 1930.
32. ———, Pollen analysis of Mud Lake bog. Ecology **12**:650–655. 1931.
33. ———, Post-glacial climate in eastern North America. Ecology **13**:1–6. 1932.
34. STARK, P., Der gegenwärtige Stand der pollenanalytischen Forschung. Zeitschr. Botanik **17**:89–125. 1925.
35. TRANSEAU, E. N., On the geographic distribution and ecological relations on the bog plant societies of northern North America. BOT. GAZ. **36**:401–420. 1903.

36. VON POST, L., Einige südschwediche Quellmoore. Bull. Geol. Institt. Upsala. Vol. 15. 1916.
37. VOSS, J., Preliminary report on the paleo-ecology of a Wisconsin and an Illinois bog. Trans. Ill. Acad. Science **24**:130–136. 1931.
38. ———, Pleistocene forests of central Illinois. BOT. GAZ. **94**:808–814. 1933.
39. WATERMAN, W. G., Preliminary report on the bogs of northern Illinois. Trans. Ill. Acad. Science **14**:79–84. 1921.
40. ———, Bogs of northern Illinois. Trans. Ill. Acad. Science **16**:214–225. 1923.
41. WILDE, S. A., The relation of soils and forest vegetation of the lake states region. Ecology **14**:94–105. 1933.
42. WILSON, L. R., The Two Creeks forest bed, Manitowoc County, Wisconsin. Wis. Acad. Science **27**:31–46. 1932.
43. WOODARD, J., Origin of prairies in Illinois. BOT. GAZ. **77**:241–261. 1924.
44. WOODHEAD, T. W., History of the vegetation of the southern Pennines. Jour. Ecology **17**:1–34. 1929.

ANATOMY OF THE VEGETATIVE ORGANS OF THE PARSNIP

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 455

WINIFRED CAROLINE WARNING

(WITH FORTY-FOUR FIGURES)

Introduction

Apparently no study of the anatomy of the parsnip has been reported, although descriptions of various tissues and organs of other Umbelliferae appear in the literature. HOFFMAN (7) and COURCHET (3) have studied the gross morphology; TRECUL (8), vessels; TRECUL and VAN TIEGHEM (9), secretory canals; VAN TIEGHEM and DULIOT (10), origin of the first group of secondary roots; and HOAR (6), stem anatomy. In some of these contributions references to the structure of the parsnip are found, but a connected study of its anatomy does not appear.

MATERIAL AND METHODS.—The material was obtained largely from seedlings and plants grown in the University of Chicago garden and partly from seedlings grown in the greenhouse. The variety used is known commercially as Hollow Crown.

Three methods of fixing were employed, Flemming's medium solution, chromo-acetic solution, and formalin-acetic-alcohol mixture. The safranin, gentian violet, orange G combination, and Haidenhain's iron-haematoxylin were used in staining.

Gross morphology

Pastinaca sativa L. is normally a biennial producing a large taproot in which much food is stored, a stem, and leaves during the first year; and leaves, a floral axis, flowers, and fruit during the second year.

The mature root is conical in shape and represents the primary root together with the hypocotyl. Four rows of shallow depressions occur on it, running almost directly downward, and secondary roots are diverged in these depressions. The stem is short and from it

diverge numerous leaf bases which are placed in a close spiral. The cotyledons are opposite but all other leaves are alternate. Juvenile leaves are simple while those produced later are compound or decompound. The blades of simple leaves vary from obovate with entire margins in the cotyledons to reniform with crenate margins and deeply three-lobed with toothed margins, while in the leaflets they range from obovate with crenate margins to deeply incised with toothed margins. All are net-veined with branches diverging from the prominent midrib, separating each leaf or leaflet into definite, rather small vein islets. The leaves are large and there is a lack of uniformity in both color and texture. They may vary from deep olive to light green in the blades, while the petioles range from dark to light or reddish green and may be coarse or fine and rather smooth or rough. The floral axis is coarse, columnar, deeply five grooved and branched, and bears numerous flowers as well as leaves. These present an increasing and decreasing series in the number and arrangement of leaflets involved. On the lower portion of the axis they are odd pinnately compound. Proceeding in the acropetal direction, they are decompound, then compound, and in the upper level vestigial.

Anatomy

A longitudinal section through a mature root shows an outer, rather thin layer of periderm and beneath it a heavy layer of phloem, consisting of phloem, phloem parenchyma, and fibers. Centripetal to this is a narrow layer of cambial cells, and at the center the xylem composed of vessels, fibers, and xylem parenchyma. In the upper portion or region of the hypocotyl a core of pith is differentiated and lies within the xylem. If a section is cut where secondary roots have been diverged, radiating strands of vascular tissue may be traced running outward and defining the position of these roots. The stem is greatly constricted in diameter and shows the same type and arrangement of tissues as are developed in the hypocotyl, but the pith has become much broader and consequently the other tissues form a very narrow band composed largely of leaf traces. A longitudinal section of the floral axis shows an epidermis, collenchyma, cortical parenchyma, a band of bundles, and a pith hollowed at the internodes. Since many of the tissues in the various organs

are similar in structure, their anatomy may be discussed under one caption.

Pith is differentiated in the hypocotyl, stem, and floral axis, and consists of large thin-walled cells with small intercellular spaces. In transverse section the cells are roughly hexagonal in outline and the intercellular spaces usually triangular, rarely rectangular. In longitudinal section they are rounded rectangular, one to two times as long as wide, with transverse walls, so that the pith is composed of cells which are somewhat barrel-shaped with hexagonal bases (figs. 19, 26).

Xylem is developed in all the vegetative organs and consists of fibers, vessels, and xylem parenchyma. The vessels are annular or spiral in the primary tissue and scalariform or reticulate in the secondary. Large vessels are porous with transverse cross walls which are sometimes somewhat oblique, while the smaller ones are pointed but porous. The xylem parenchyma cells are thin-walled and, as seen in transverse section, are hexagonal in outline when young but become much distorted as they enlarge, presenting various forms (figs. 33–41). In longitudinal section they are elongated and pointed at the ends. The walls are pitted, both simple and bordered pits occurring, depending upon the age of the cells.

Phloem develops in all vegetative organs and is composed of sieve tubes, companion cells, phloem parenchyma, and fibers (figs. 2, 42). The sieve tubes as seen in transverse section are small, thin-walled, and hexagonal in outline; in longitudinal section they are greatly elongated with sieve plates on the sides and ends, and are essentially rectangular with transverse walls. The companion cells are as long as the sieve tubes and in transverse section are pentagonal, quadrangular, or triangular. The phloem parenchyma is thin-walled, roughly hexagonal in cross-section, and a polygon of from four to nine sides in longitudinal. The cells are therefore rather regular polyhedrons with faces varying in number within a narrow limit, and are practically isodiametric. Those near the periphery of the root and hypocotyl are much smaller and heavier-walled than are the cells farther removed.

Collenchyma occurs in the stem, floral axis, and leaf, and the groups are usually reniform in outline and consist of cells with heavy

walls and much heavier thickenings at the corners. In transverse section the cells are hexagonal when young but become rounded as the walls thicken, always showing prominent round nuclei; in longitudinal section they are several times longer than wide, with cross walls transverse or oblique and the nuclei broadly lenticular (figs. 22, 26, 31).

Cortical parenchyma is differentiated in the petiole and floral axis and is of two types, an outer zone of areas beneath the epidermis and an inner zone. The subepidermal groups of cells are photosynthetic, all of them containing numerous chloroplasts. The walls are thin and in transverse section the cells are small and roughly hexagonal in outline; in longitudinal section they are slightly rounded and somewhat longer than wide, with essentially transverse walls at intervals bounding intercellular spaces which are connected with stomatal cavities. The inner, non-photosynthetic zone consists of large, thin-walled cells which in cross-section are hexagonal with small intercellular spaces. In longitudinal section they are rectangular, much longer than wide, with transverse walls (figs. 22, 26).

The cortex of the root, hypocotyl, and stem resembles the cortical parenchyma and in cross-section consists of thin-walled cells, hexagonal in outline, with small triangular, rarely quadrangular intercellular spaces which are not distinguishable when the tissue is young, but are apparent when it becomes older (fig. 1). In longitudinal section the cells are rectangular and almost isodiametric, with transverse walls.

Sclerenchyma in the form of fibers occurs in all the vegetative organs. In transverse section the cells are small, heavy-walled, and hexagonal in outline; in longitudinal section they are narrow and much elongated, with pointed ends. Normally in the root and hypocotyl they are not lignified during the first year but become very woody during the second; in the other organs they lignify early, this being particularly true of the floral axis (figs. 22, 26, 42).

The epidermis of the different organs varies somewhat according to its several functions. That developed on the primary root, stem, and hypocotyl consists of a single layer of practically isodiametric cells with a somewhat rounded outer wall, the cells being broadly rectangular in longitudinal section. The epidermis of the petiole,

veins, and floral axis is similar in transverse section and consists of a single layer of heavy-walled, essentially isodiametric cells with collenchymatous thickenings in the corners; in longitudinal section it consists of slightly rounded cells three to four times as long as wide, with transverse walls; in face view the cells are tabular (figs. 22, 24, 26, 27). The epidermis, which is differentiated on the portions of the leaf blades between the veins, differs in some respects from that covering the veins. In transverse and longitudinal sections its cells appear similar in outline to the tabular, but in face view the walls are tortuous (figs. 24, 25).

Periderm is differentiated on the root, hypocotyl, stem, and regions which have been injured, and is initiated after the sloughing of the outer tissues in the root and hypocotyl, while in the stem it follows the desiccation of the leaf bases. The cork which develops on the root and hypocotyl is very regular. In transverse section it consists of closely packed, thin-walled, rather small rectangular cells from two to three times as long as broad, and in longitudinal section it is rather similar (figs. 5, 6, 32). The periderm which develops on the stem and places of injury consists in cross-section of heavy-walled, rounded, almost isodiametric cells.

Cambium is differentiated in all the vegetative organs and in transverse section is composed of small, thin-walled, closely packed, fairly rectangular cells with round nuclei. In longitudinal section the cells are much longer than wide, with transverse or sometimes somewhat oblique walls and having elongated lenticular nuclei containing one or two prominent nucleoli (figs. 43, 44).

The oil ducts which are cut off from the pericycle and primary phloem are described under the discussion of ontogeny. Other canals are differentiated in the phloem parenchyma, phloem of bundles, pith, and cortical parenchyma. In transverse section the duct is a polygon of varying number of sides, while the epithelial cells are usually pentagonal and smaller than the adjacent cells. In longitudinal section the canal is much elongated and at times interrupted. Its roughly rectangular epithelial cells vary from isodiametric ones to those several times longer than wide and are characterized by large, rounded nuclei and dense protoplasm (figs. 7, 9, 10). Oil ducts rarely anastomose, but this may occur when tissues are reoriented or when cells are rapidly increasing in size, as in the petiole and root.

Two canals may be oriented so that their epithelial cells touch, and in case the intervening walls break down, a canal is formed which is elliptical in cross-section and much broader than usual in longitudinal section.

Striations are developed on all tabular cells and in transverse section are short triangular projections consisting of minute conical protuberances, transparent and somewhat iridescent, lying in longitudinal rows which are more or less parallel and occur at intervals of from seven to twelve striations per cell (figs. 21, 22, 24, 26).

Hairs occur on tabular cells on the ridges of the petiole and floral axis, and on the veins and margins of leaves. They are of two types, a straight, slender, conical form and a shorter, curved, heavier-walled type (figs. 29, 30). Both forms are transparent and iridescent with a large nucleus near the center. Their surfaces are closely beset with the same type of conical protuberances which form the striations, and it seems probable that these protuberances as well as the hairs may be responsible for the skin irritations which result from handling parsnip leaves, as reported by BLANCHARD (2) and others. The number of hairs per unit area varies with the age and size of the organ on which they are developed.

Stomata are differentiated on the stem, leaf, and floral axis. The stomata of the petiole and floral axis are confined to the grooves and are very numerous (figs. 27, 28). Naturally few are developed on the sheathing portion of the leaf bases, and on the blade they are limited to the cells with tortuous walls where they occur on both sides of the leaf, being somewhat more numerous on the lower than on the upper surface, and less widely separated in young than in older tissue. The stomata are of the common mesophytic type with guard cells which contain many plastids. The stomatal cavities vary in size, depending upon the organ in which they are differentiated, being small in the stem, floral axis, petiole, and cotyledons and much larger in the blade (figs. 21, 22, 24, 25, 26). Relatively few appear on the stem, and those which persist over the growing season develop into lenticels which are of the ordinary type, with a heavy periderm, ramifying intercellular spaces, and a relatively small number of complementary cells. The closing cells break down early in the spring of the second year and the lenticels gradually disintegrate.

Ontogeny

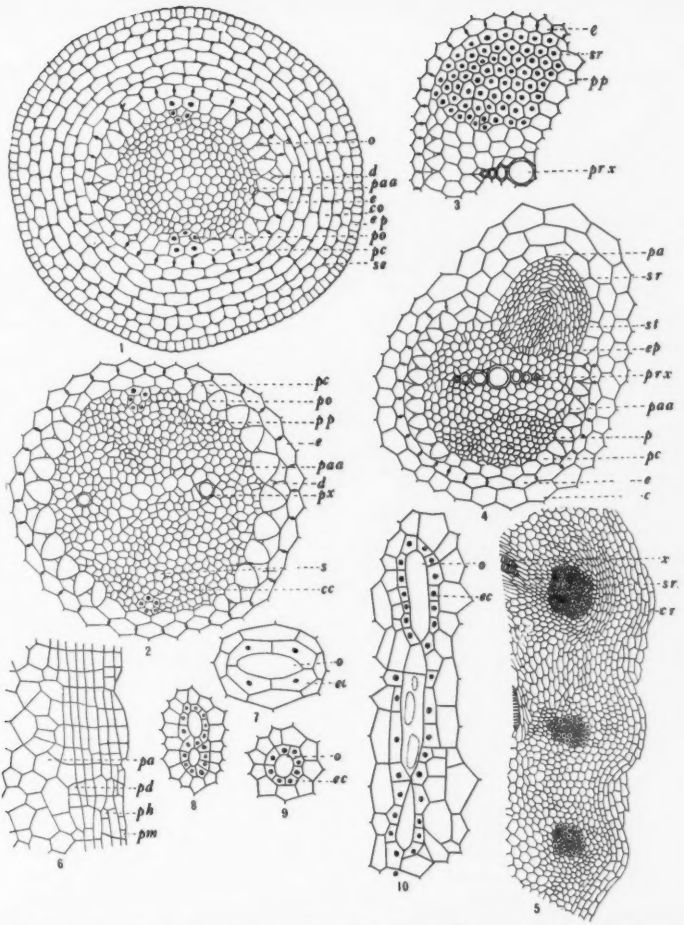
Three regions appear in the young seedling: root, hypocotyl, and cotyledons. The junction of the root and hypocotyl is readily distinguished, being marked by an enlargement of the hypocotyl and an abrupt constriction of the root. Small ephemeral root hairs develop and secondary roots are diverged. The stem is not distinguishable in the earliest stages, and the cotyledons are small.

Primary root and hypocotyl

The primary root falls under Janczewski's third type, plerome and periblem defined with periblem overlying the plerome, while calyptrogen and dermatogen are differentiated together.

Since the seed is slow in germination, many of the earlier stages must be studied while the plant is still within the fruit coat. A transverse section through the proximal part of a root which has been in process of germination for three days shows a mass of undifferentiated cells, and at four days the epidermis consisting of a single layer of cells is differentiated (fig. 1). At five days the pericycle is readily distinguished. In transverse section it is composed in its earliest stages of a single row of isodiametric, hexagonal cells much larger than any of the others, while longitudinally the cells are broadly rectangular. The cortex, consisting of from seven to ten rows of relatively large cells, is thus set off from the central meristem, and the endodermis, composed of a single row of cells, isodiametric and hexagonal and smaller than those of the pericycle, is distinguishable. In longitudinal section the latter are rectangular and little longer than wide, and because of the dense protoplasmic content the Casparian strips, which are never very heavy, are not easily distinguished. When the cells lose their protoplasm, however, they are seen to consist of radial thickenings with a small lenticular expansion at the center of the wall (figs. 1, 2). During the fifth and sixth days the cells of the pericycle divide rapidly, and the resulting walls may be oblique, tangential, or vertical. The vertical and obliquely longitudinal divisions serve to increase the number of cells in the pericycle, the tangential divisions producing endodermal cells and the oblique ones usually forming oil ducts.

The first secretory canals which are differentiated and in which



FIGS. 1–10.—Fig. 1, transverse section of young seedling root showing early stages of primary tissues with pericyclic oil ducts differentiated and phloem oil canals abutting on pericycle, ×220; fig. 2, cross-section through young hypocotyl showing protoxylem points, sieve tubes, companion cells, and phloem oil ducts one cell removed from pericycle, ×220; fig. 3, transverse section of primary root with meristem of secondary showing position of root, primary xylem, and unruptured endodermis, ×440; fig. 4, cross-section showing older secondary root with endodermis partially disintegrated, ×220; fig. 5, transverse section of older root showing origin of second and later groups of secondary roots in pericyclic periderm, ×220; fig. 6, longitudinal section of periderm, ×220; fig. 7, transverse section of oil ducts, primary type, ×440; figs. 8, 9, some types found in secondary tissues, ×110; fig. 10, longitudinal section of oil duct, ×110 (*cc*, companion cell; *co*, cortex; *cr*, cork; *d*, central oil duct; *e*, endodermis; *ec*, epithelial cell; *ep*, epidermis; *o*, oil duct; *p*, phloem; *pa*, parenchyma; *paa*, primary parenchyma; *pc*, pericycle; *pd*, periderm; *ph*, phellogen; *pm*, phellem; *po*, phloem oil duct; *pp*, primary phloem; *prx*, primary xylem; *px*, protoxylem point; *s*, sieve tube; *se*, intercellular space; *sr*, secondary root; *st*, stele; *x*, xylem).

pericyclic cells alone are involved are formed in the following manner: Beginning with the central pericyclic cells, which are located at points 180° apart, from two adjoining sides of two adjacent cells quadrilateral sections are cut off. Divisions follow on both sides of the central cell, quadrilateral sections are cut off (to the right on one side and to the left of the central duct on the other) until two arcs of from 11 to 15 cells are formed on opposite sides of the root. Schizogenous splits develop as mitosis proceeds, and the central canals develop. In transverse section these are quadrangular, being bounded by two of the small quadrilateral and two of the larger hexagonal cells which function as epithelial cells. All other pericyclic ducts are triangular, being limited by one of the small quadrilateral and two of the larger hexagonal cells, and a gradual diminution in size from the center to the end of the arcs is apparent (figs. 1, 2). The number of epithelial cells bounding the pericyclic oil ducts seems never to be increased by mitosis, and consequently these canals remain distinct from those which are differentiated later. The protoplasm of the epithelial cells is dense at first and the nuclei are prominent, but as the cells grow older they gradually grow faint and the ducts probably become functionless. In longitudinal section the epithelial cells are rectangular and isodiametric, and no anastomosis of pericyclic oil ducts was observed. There are two groups of from four to five pericyclic cells lying centrifugal to the primary phloem which do not divide to form oil canals, retaining their hexagonal outline (figs. 1, 2). The order of pericyclic cell division just described has been adopted for the sake of convenience. While the central cells are usually the first to divide, exceptions occur, and individual cells or one of the arcs may divide irregularly or be retarded in division. Development of the pericyclic oil duct was first discussed by TRECUL (**8**), and the results of this study differ from his conclusions in no essential respect.

Concomitant with the development of the pericyclic oil canals is the differentiation of the primary phloem. Two protophloem points, 180° apart and located opposite the middle of the non-secretory pericyclic cells (and removed from them by two or three cells in the centripetal direction), enlarge and mitosis follows, in which small cells are cut off, thus differentiating the first sieve tubes and com-

panion cells. Divisions follow rapidly; protophloem is followed by metaphloem; and two groups of primary phloem are developed which are elliptical in outline and limited by the pericycle and parenchyma.

While the metaphloem elements are still in process of differentiation, two cells 180° apart, abutting on the pericycle and near the center of the protophloem, gradually lose their protoplasm through the disappearance of the comparatively small nucleus, followed by the cytoplasm, leaving a clear lumen. The cells which are adjacent to them, two pericyclic and three phloem, now become densely protoplasmic and the central cells function as oil canals while the adjacent ones become epithelial (fig. 1). Infrequently two adjoining cells lose their protoplasm but the wall separating them fails to disintegrate and two adjacent oil ducts are thus formed. These phloem ducts function for a short time only, and usually cannot be distinguished after the cortex has disintegrated.

Before the metaphloem has fully matured, two procambial cells, lying directly opposite the central oil ducts and separated from them by two or three parenchymatous cells, are differentiated from the central meristem and mature into the first elements of the protoxylem. Development of the primary xylem proceeds centripetally, until the metaxylem cells meet at the center to form the diarch xylem plate which consists of from seven to nine cells and contains fewer cells than the primary phloem. The primary xylem is surrounded by parenchyma which separates it from the other tissues.

There are no marked differences between the epidermis, cortex, endodermis, and pericycle of the primary root and hypocotyl, except that the number of cells in each tissue in the latter is greater, resulting in all probability from the increase in diameter. The phloem of the lower portion of the hypocotyl is similar to that of the root, but in the upper levels the phloem oil canals are differentiated one cell removed from the pericycle, while in the root they abut directly upon it and the intervening cells are of pericyclic origin (fig. 2). Two protoxylem points appear as in the root, and these are rapidly followed by others until two groups of from four to five cells are developed. In the root centripetal growth completes the xylem plate, but in the hypocotyl this does not take place because the

procambial cells fail to mature into xylem but remain parenchymatous, and this central parenchyma by cell division and growth develops into the pith (figs. 12–14, 19). The change in orientation of the xylem and phloem of the hypocotyl is discussed under the section on transition.

Triarch condition

The primary xylem of the root and hypocotyl is normally diarch, although a few exceptions appeared, for in the several thousands of plants which were studied seven were found with a portion of the primary xylem triarch and in every case triple cotyledons developed. Five of these plants were available for close study, one in the initial and four in more advanced stages of growth. Since no discussion of such structures was discovered in the literature, and since triarchs have been tested for heritability of the arch condition, a brief statement concerning the anatomy seems desirable. It is freely admitted that absolute conclusions cannot be deduced from so small an amount of material, but in any species the condition seems to be of rare occurrence and in all probability a number of species must be studied to arrive at a satisfactory explanation.

In the initial stage, or when the plant is still within the fruit coat and there exists no definite demarcation between root and hypocotyl, the triarch structure appears at a considerable distance above the root tip and in all probability is restricted entirely to the hypocotyl. The pericyclic and phloem oil ducts as well as the protoxylem points are differentiated in their normal order, number, and position in the root, but one protoxylem point appears in advance of the other. As the level of the hypocotyl is reached and soon after the second protoxylem point has developed, a third phloem oil canal is differentiated. This appears a short distance above the level of the xylem point and is separated from one of the first two phloem oil ducts by four or five cells.

These four or five intervening cells and those adjacent to them centripetally, as well as the non-secretory pericyclic cells located centrifugally, soon become densely protoplasmic and rapid cell division follows, causing the portion of the stele involved to bulge slightly into the cortex. Concurrently with these changes there occurs a wider separation of the phloem oil ducts and a crowding of the peri-

cyclic oil canals and the protoxylem points, so that eventually they appear on an arc approximately 120° apart. A third central pericyclic oil canal and about one half of the normal number of pericyclic oil ducts are now differentiated on the longer arc midway between the other two. A third protoxylem point is developed at a level considerably above the third central oil duct, and three cotyledons appear which are normal in all respects with the exception that they lack one oil duct.

Four plants in a later stage of development were studied, and in all of them the primary xylem remained diarch throughout the extent of the root and the triarch structure became apparent in the lower portion of the hypocotyl, at the level where the bundles were being differentiated before transition. One bundle was perfectly normal, but as the bifurcation was about to be formed in the other, the two xylem arms swung apart and were oriented at right angles to each other with one arm following the bifurcation curve and the other extending in a radial direction, thus forming the triarch.

Development of the oil canal did not coincide in the four hypocotyls, for in three of them there were three groups of pericyclic oil ducts, two containing the normal number of cells and one with fewer than usual, while in the fourth there were two groups of perfectly normal oil ducts. In this particular case a group of phloem cells was differentiated centripetal to the pericyclic oil canals, a most unnatural position. A third phloem oil canal could not be distinguished in any of these roots, but these ducts are ephemeral and soon become unrecognizable. The transition followed the usual lines, except that the halves of the split bundle did not form a normal bifurcation (fig. 19). The cotyledons were normal with two exceptions: in one no oil ducts accompanied the lateral bundles and in another one lateral bundle did not divide until the middle of the cotyledons was reached, thus causing two of the cotyledons to adhere up to this point. In two of the hypocotyls secondary roots were differentiated while transition was in progress, and three of the plants were belated in germination.

It is evident that the abnormal structure in the plants studied was largely if not entirely confined to the hypocotyl, for in every case the root was diarch throughout practically all of its extent, and this coincides with HILL'S (5) work on *Piper*. The third xylem arch in

each plant is always the result of splitting instead of bifurcation during transition, and various irregularities follow, differing in each plant. It seems apparent that the so-called triarchs are not triarch but diarch, in which one bundle is split at or near the time of transition; and this agrees with the results of plant breeders who have found that the triarch structure is not heritable. The cause of the abnormality is difficult to trace, but it is possible that differentiation of secondary roots in the hypocotyl and belated germination may be contributing factors. That true triarchs were not found does not in any way assume that they do not occur; but if they appear a cursory examination should reveal their structure, for six groups of secondary roots should be differentiated and a section near the root tip should show the triarch xylem plate. Moreover perfect triple cotyledons should be diverged and naturally no irregularities in structure would be expected. It is again emphasized that no definite conclusions can be drawn from the few cases studied; this report is merely a contribution to clear up a puzzling situation which seems to have been misinterpreted.

Lateral roots

The lateral roots are of two types, permanent and transient. The former are differentiated in the pericycle of the primary root before disintegration of the outer tissues. They persist throughout the life of the plant and are few in number. The transient laterals are also of two types, the first of which is initiated in the same manner as the permanent ones but persists only until the cortex sloughs; the second is differentiated in the pericyclic cork during any active period and is of short duration.

Since the primary root is diarch, the secondary roots are developed at points which are located near the limits of the non-secretory pericyclic cells; but at any level only one root is initiated. When a root of the permanent or of the first type of transients is about to be differentiated, a single cell of the pericycle becomes meristematic, enlarges, and mitosis follows. In cross-section the first cell divisions are tangential, followed by radial and tangential ones and then those in various directions, and the root is developed following the lines of the primary. As it enlarges it ruptures the endodermis, cor-

tex, and epidermis, and as it proceeds apparently absorbs two or three layers of cortical cells and a connection is made with the primary xylem (figs. 3, 4). The second type is initiated in groups after the endodermis, cortex, and epidermis have disintegrated and secondary tissue has developed, and is differentiated near points where transient roots sloughed, thus leaving the conductive tissue free. The phellogen in these regions becomes meristematic and there is an unusual proliferation of periderm, followed by development of initial cells in the phellogen in proximity to the conductive strands. The development of these roots does not differ from that of the secondaries, except that they rupture the periderm as they grow outward (fig. 5). The permanent and first type of transient laterals are endogenous in origin, but the second type of transients can be considered so only in the sense that the periderm in which they are initiated is derived from the pericycle, which was endogenous although the cork is peripheral and a part of the secondary body when these roots are differentiated.

The number of lateral roots which may be developed in association with the free conductive tissue of a secondary one depends upon the size of the conductive strand. Since this gradually increases, the number during the first year is much smaller than during the second year when fascicles of over one hundred are frequently developed. While some of these diverge from the lower part of the main root, by far the greater number appear on the upper portion. In general structure laterals are similar to those of the primary root, but the cells of the phloem and parenchyma are relatively fewer in number while those of the xylem are greater. The arch condition of the first group of laterals usually conforms with that of the primary, but because of the excessive xylem there is a crowded condition, since fourteen or more cells are involved and the xylem frequently abuts on the pericycle. Two or three more or less parallel rows of rather perfect triarch or tetrarch roots may appear.

Stem

The structure of the stem is similar to that of the hypocotyl until the lateral cotyledonary traces are differentiated and the cotyledonary plate defined. The growth of the traces, together with the re-

orientation of bundles, forces the pericyclic oil ducts outward, then separates them into groups and single canals, and finally they become indistinguishable. The endodermis is ruptured, and concomitantly the tissues lying centripetal to the bundles become meristematic and leaf traces are rapidly developed, thus setting off the pith. When the tissues are young the bundles are discrete but become crowded as leaf traces continue to be differentiated. The cortex is relatively narrow, consisting of from six to seven rows of cells when the plant is young, and gradually increasing as it grows older. The stem is shallowly five-grooved, and colenchyma is developed in the ridges and hairs on the surface when young, disappearing as the leaf bases are diverged. The upper concave portion remains meristematic during the winter and is protected by leaf bases and covered with small young leaves which, because of their close packing and dense covering of hairs, are frost resistant. In the spring these develop into basal leaves.

Cotyledons

The short petiole of the cotyledons is reniform in transverse section when young, but becomes slightly three-lobed on the abaxial side as it grows older. It is from seven to eleven cells in thickness, consisting of a single layer of epidermal cells and a cortical parenchyma which is traversed by three bundles whose origin is discussed under transition. One large oil duct separated from the phloem by a few parenchyma cells is associated with each of the bundles, and a smaller canal is developed near the xylem of the median bundle (fig. 16). A single row of epidermal cells is differentiated on the blade, and below it on the upper side a layer of rounded palisade cells appears. The spongy mesophyll lies directly beneath and all palisade and mesophyll cells are densely filled with chloroplasts. The three bundles which enter the blade branch at various intervals, and as they ramify one oil duct is developed with each branch. The cotyledons persist only until four or five leaves appear, when they are overshadowed and desiccation follows.

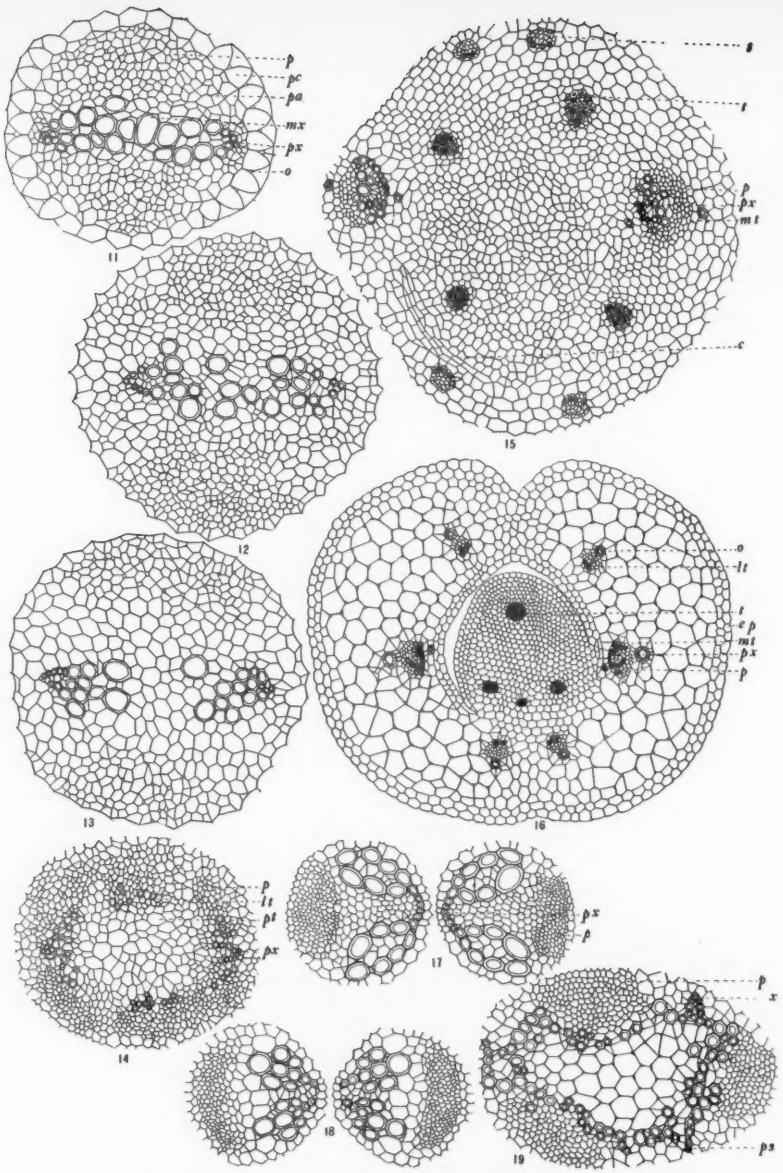
Exarch-endarch transition

The transition region is initiated in the lower portion of the hypocotyl and terminates in the petioles of the cotyledons. There is a

gradual and simultaneous reorientation of the elements involved, until they appear on a curve 180° from their original position. The first evidences are noticeable when a narrow bifurcation of the protoxylem appears while the metaxylem retains its central position (fig. 11). At a slightly higher level the bifurcation is broader as the protoxylem is differentiated outward and the metaxylem laterally, so that each bundle now consists of two strands with one strand of each oriented on a clockwise curve and the other on a counter-clockwise curve from the original position. A parenchyma, which is destined to become the pith, appears in the central region (figs. 12, 13). At the level of the cotyledonary plate, the xylem has been oriented so that the curve is approximately 30° from the original position; and at the level where the meristem of the stem is cut off from the cotyledons, the xylem of the bundles has been gradually oriented to the tangential or 90° from its original location (fig. 15). After the tangential stage, the transition occurs in the petioles of the cotyledons. In the lower portion of the petioles, the xylem has been oriented on a curve of from 90° to 135° from the central position, and some distance above this the true endarch condition or 180° from the original position is reached (figs. 16–18).

The primary phloem is also reoriented during transition. In the root and lower hypocotyl it is differentiated in a radial position with respect to the primary xylem; at a higher level of the hypocotyl a bifurcation of the two phloem bundles occurs and the halves of each bundle are gradually oriented on clockwise and counter-clockwise curves until they lie adjacent to the metaxylem, and each phloem bundle appears in a position lateral to the xylem strand nearest it (figs. 11–14). Differentiation along the same curves continues until the phloem is gradually oriented so that each strand lies on the same radius with the xylem strand nearest it, and typical collateral bundles are thus formed (figs. 15–18). These bundles are the median cotyledonary traces.

The cotyledonary plate is distinguished from the hypocotyl by the differentiation in the procambial cells of two groups of two bundles each, lying 180° apart and in radial position to the transition bundles, from which they are separated by a narrow band of parenchyma (fig. 14). The bundles in each group are at first closely



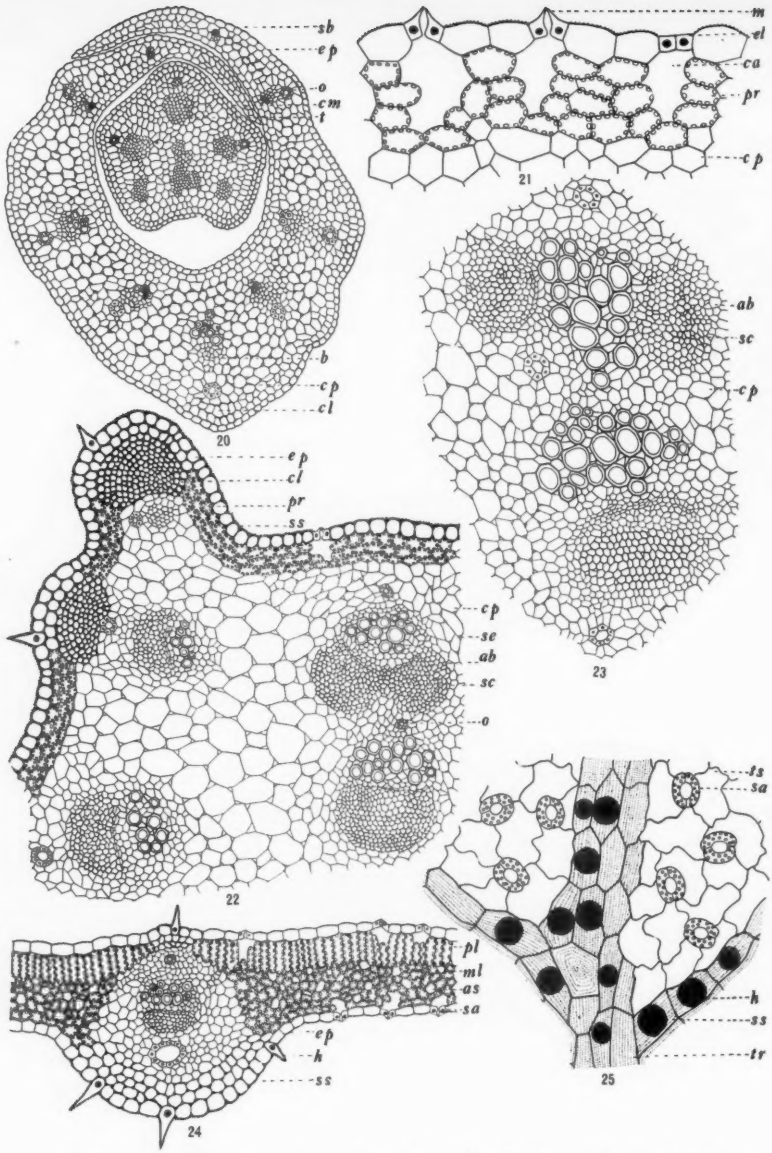
FIGS. 11–19.—Fig. 11, transverse section of lower hypocotyl showing first stage in transition, × 550; fig. 12, cross-section of hypocotyl with metaxylem oriented in a more lateral position, ×550; fig. 13, transverse section of upper hypocotyl showing change in orientation of xylem and differentiation of pith, ×550; fig. 14, cross-section of cotyledonary plate showing reorientation of xylem and phloem and differentiation of lateral cotyledonary bundles, ×220; fig. 15, transverse section showing orientation of transition bundles as cotyledons are being differentiated from central meristem, ×160; fig. 16, cross-section of cotyledons and central meristem with transition bundles tangential, ×220; fig. 17, transverse section of transition bundles in petioles of cotyledons almost endarch, all other tissues omitted, ×440; fig. 18, cross-section of transition bundles in petioles of cotyledons with xylem in endarch position, ×440; fig. 19, transverse section of cotyledonary plate showing orientation of triarch bundles in transition, ×440 (*c*, cambium; *ep*, epidermis; *ll*, lateral cotyledonary bundle; *mt*, median cotyledonary bundle; *mx* metaxylem; *o*, oil duct; *p*, phloem; *pa*, parenchyma; *pc*, pericycle; *ps*, separated xylem arm; *pt*, pith; *px*, protoxylem point; *t*, leaf trace).

associated with each other but are soon separated by a few parenchyma cells which develop between them. All of the parenchyma gradually broadens, and at successively higher levels all bundles are separated by increasingly broader bands of this tissue. As the cotyledons are diverged from the stem, two bundles, one from each group, pass into each cotyledon and become the lateral cotyledonary traces (figs. 15–18). These bundles are developed with endarch arrangement of their elements and take no part in the transition.

Leaves

When the base of a young leaf is diverged from the stem it is roughly crescent-shaped, with overlapping ends, and at this early stage there is no distinction between its tissues except that the bundle meristems consist of cells which are densely protoplasmic and much smaller than those surrounding them. The base increases rapidly in size and at the same time tissues are reoriented and mature. The epidermis is differentiated and collenchyma develops beneath the ridges, being limited by the photosynthetic cortical parenchyma which is centripetal to the grooves and consists of from three to four layers of cells (figs. 20, 23, 27). A continuous zone of cortical parenchyma develops centripetal to these tissues and occupies the center of the petiole, thus surrounding the bundles.

Concomitant with the development of the various tissues is that of the bundles, which are initiated in groups and are gradually separated by the parenchyma which is differentiated between them. At the same time they are gradually reoriented so that eventually they are located at regular intervals around the base, with the xylem facing the ventral and the phloem the dorsal side. At the center from one to three bundles appear, depending upon the size of the base; and on either side of these, small and large bundles alternate with both types, gradually decreasing in magnitude as the ends are approached (fig. 20). As this diminution in size is progressing, the xylem cells, always fewer in number than the phloem, are differentiated less frequently and the bundles which normally are collateral may be reduced to phloem only. Sclerenchyma, in the form of caps, is developed as the bundles mature, with a heavy cap at the xylem and a smaller one at the phloem pole. Oil ducts are associated with all of the bundles but are always separated from them by a few



FIGS. 20–25.—Fig. 20, transverse section of sheathing leaf base and central meristem showing arrangement of bundles, ×110; fig. 21, transverse section of portion of petiole with stomata and stomatal cavities, ×550; fig. 22, cross-section of portion of petiole showing position and anastomosis of bundles, ×220; fig. 23, transverse section of central portion of petiole with several bundles anastomosing, ×220; fig. 24, cross-section of portion of leaf showing small vein and photosynthetic cells, ×220; fig. 25, surface view of leaf with two types of epidermal cells and position of hairs and stomata, ×220 (*ab*, anastomosing bundles; *as*, air space; *b*, bundle; *ca*, stomatal cavity; *cl*, collenchyma; *cm*, central meristem; *cp*, cortical parenchyma; *el*, section through end of stoma; *ep*, epidermis; *h*, hair; *m*, median section of stoma; *ml*, mesophyll; *o*, oil duct; *pl*, palisade cell; *pr*, photosynthetic parenchyma; *sa*, stoma; *sb*, sheathing leaf base; *sc*, sclerenchyma; *se*, intercellular space; *ss*, striation; *t*, leaf trace; *tr*, tabular cell; *ts*, tortuous cell).

parenchyma cells. In juxtaposition to the central bundle there may be as many as four oil canals; other large bundles are associated with two ducts, a small one near the xylem and a larger one between the phloem and the groove of the collenchyma; while one duct near the phloem appears near small bundles. All of these ducts are schizogenous in origin and develop when the tissue is still in a meristematic stage. Usually four cells which are centered about a common point become densely protoplasmic; and a split, minute at first but gradually increasing in size, separates them at the central point, forming a small canal with the four bounding cells functioning as epithelial cells. As the latter divide the duct is enlarged.

There is a gradual constriction of the leaf base in the acropetal direction. As it merges into the stalk of the petiole, the central portion becomes broader and the ends are restricted, while the groove becomes very shallow and may be eliminated entirely if collenchyma is developed in the adaxial side. In this way the stalk is rounded with a very shallow groove or flattened surface on the ventral side.

The tissues of the stalk are similar to those of the base, except that the photosynthetic parenchyma is broader and contains more plastids (fig. 22). The arrangement of the bundles varies considerably, for as the petiole is constricted there is a reorientation, so that some are located about the periphery with the protoxylem centripetally placed while others appear in the central parenchyma with the xylem directed toward the ventral side. A row of from two to five bundles appears at the middle of the parenchyma and other rows are found on either side of this, varying in number and magnitude according to the size of the petiole. While reorientation is in progress many changes occur in the magnitude and relative position of the tissues of the bundles, for they separate and anastomose frequently. When the change to the stalk is completed the peripheral bundles are relatively stable in size, shape, and position; but those centrally placed continue to separate, reorient, and anastomose throughout the length of the petiole. Since the bundles are differentiated in groups in the base, they tend to separate and then anastomose, thus evolving various types. Those consisting of phloem or sclerenchyma occur frequently, while those consisting of xylem are rare and all three

types may be developed by the separation of small portions of tissue from the main mass. Bicollateral forms are common and are evolved when two bundles of essentially the same magnitude anastomose. The xylem cells unite, which seems to be a common tendency in spite of the fact that a reorientation of 180° is sometimes necessary, while the phloem appears on either side of the xylem and the xylem sclerenchyma caps have become weak and are gradually developed in lateral positions (fig. 23). Amphicribral types are formed by the anastomosis of from three to eight bundles, with the xylem uniting at the center and the phloem groups partially or wholly surrounding them; amphivasal types are rare and are evolved when anastomosed traces pass out of the petiole or midrib into the leaflets. The xylem is oriented about a group of phloem cells and an amphivasal type results. It is possible to confuse compound collateral bundles with simple collaterals, but they can usually be distinguished by the excessive number of associated oil ducts and the slight irregularities in the position of tissues. They are developed when bundles are so oriented that the xylem and all like tissues anastomose laterally (fig. 22).

Anomalous types are exceedingly common and present unusual arrangement of tissues. Two of these are of such frequent occurrence that a brief description seems permissible.

One type is formed during the anastomosis of a compound collateral or bicollateral bundle, when a few of the xylem cells are separated from the main group and are forced out between the phloem cells, so that when anastomosis is completed there are either one or two small groups of xylem extraneous to the phloem and 90° from the main mass. The second type is evolved when the phloem sclerenchyma caps are gradually oriented between the phloem and some of the xylem, and phloem cells are differentiated outwardly, so that the sclerenchyma is surrounded by phloem (fig. 23).

It is impossible to enumerate with any degree of accuracy the number of bundles in any petiole, but a rough estimate may be made from the position of the various tissues and the number of associated oil ducts. The leaf traces increase in number with the magnitude of the petiole, being five in the first leaf and conservatively estimated at fifty in the large leaves.

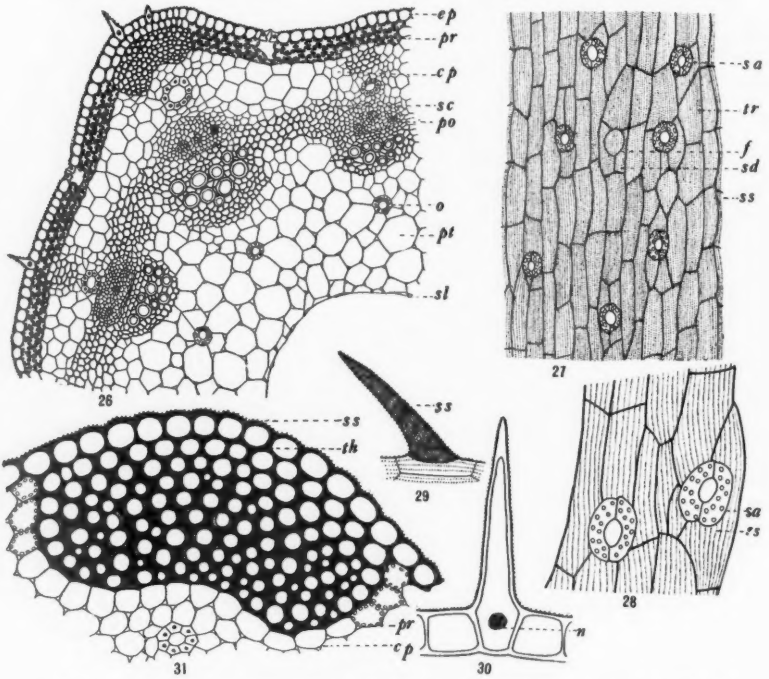
The meristem of the young leaflet resembles that of the petiole, since there is no clear distinction between the tissues save that the bundle meristem is denser; but growth is rapid and there is a simultaneous development of all elements. The epidermis is similar on the upper and lower surfaces. Beneath it on the upper side, and limited by the tissues connected with the veins, a row of palisade cells is differentiated. These are rounded, much longer than wide, and densely filled with chloroplasts (fig. 24). The mesophyll is composed of relatively small, somewhat angular cells, all containing chloroplasts and interspersed with air passages which are connected with stomatal cavities. The vascular tissue which ramifies through the leaf consists of bundles surrounded by closely packed parenchyma. Sclerenchymatous caps are developed on both poles, and oil ducts are associated as in the petiole. The reorientation and anastomosis of bundles which occurs in the petiole continues throughout the midrib.

Floral axis

The floral axis is differentiated during the first year but normally exists as a meristem until the spring of the second. The epidermis, photosynthetic cortical parenchyma, and collenchyma differ in no essential features from those of the petiole, since the structure and relative position are similar. The cortical parenchyma, however, is limited centripetally by the bundles, which with the intervening sclerenchyma form a band whose undulations follow the ridges and grooves of the outer surface. Within this band the broad central pith is differentiated. The bundles are similar to those of the petiole, except that oil ducts are always developed within the phloem while in the petiole they could be traced in rare instances only, probably owing to reorientation and anastomosis which are not nearly so marked in the axis. When the bundles are initiated they are discrete, but a meristem which rapidly becomes sclerenchymatous develops between them. Their number and magnitude vary, and large and small bundles alternate, the former being developed centripetal to the ridges and the latter to the grooves.

Oil canals are associated with the bundles, but those near the xylem are differentiated in the pith, and as the axis grows older, the epithelial cells lose their dense protoplasm and appear to be func-

tionless. The oil ducts which are developed in the phloem are usually three in number, and are bounded by four, rarely five, epithelial cells which seem to be incapable of mitosis, resembling the pericyclic canals in this respect. The pith loses its power of cell division early in ontogeny, and as the axis increases in size, the walls of its cells



FIGS. 26–31.—Fig. 26, transverse section of portion of small, mature floral axis showing tissues and schizogenous split, ×220; fig. 27, surface view of floral axis showing striations and stomata, ×220; fig. 28, detail of fig. 27 showing twin stomata, ×550; fig. 29, surface view of hair, ×440; fig. 30, section of hair showing internal structure, ×550; fig. 31, transverse section of collenchyma, ×220 (*cp*, cortical parenchyma; *ep*, epidermis; *f*, initial cell; *n*, nucleus; *o*, oil duct; *po*, phloem oil duct; *pr*, photosynthetic parenchyma; *pt*, pith; *sa*, stoma; *sc*, sclerenchyma; *sd*, subsidiary cell; *sl*, schizogenous split; *ss*, striation; *th*, collenchymatous thickening; *tr*, tabular cell).

stretch. Eventually those at the center become weak and are ruptured, and a schizogenous split results, leaving the peripheral cells intact (fig. 26). This split occurs in the internodes only, for the

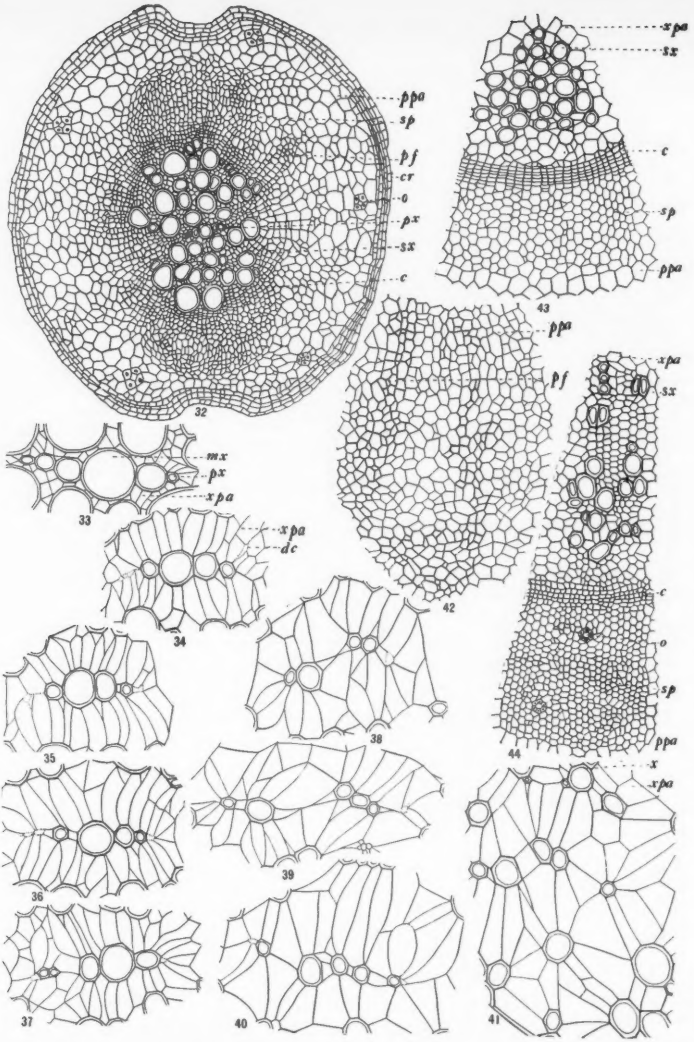
tissue at the nodes is continuous, since it defines the region where the leaf traces depart. Lignification of the floral axis commences as the fruits are maturing, beginning in the acropetal region and proceeding basipetally. The entire vascular band becomes woody and brittle, and this in all probability assists in the distribution of fruits, since the umbels and umblets are broken off soon after the fruits ripen and are carried by the wind in the same manner as are tumbleweeds.

Secondary growth

In the root and hypocotyl, secondary growth commences with the enlarging of the first leaves, or about seven days after the plant has emerged from the ground, and follows the usual lines. A cambium is differentiated in the procambial strands centripetal to the primary phloem and develops rapidly. There is a lateral extension through the parenchyma which separates the primary phloem from the xylem. In this way the cambial cells are united in the pericycle opposite the protoxylem points, thus forming the cambial ring. Xylem and phloem are laid down in the usual manner but much of this secondary tissue remains in a parenchymatous condition during the first year. In the other organs a cambium is differentiated from the procambial cells in the bundles early in ontogeny.

Secondary thickening in the root and hypocotyl naturally pushes the pericycle, endodermis, cortex, and epidermis outward; and when pressure from within is sufficient, they are stretched and weakened, and since cell division and growth have ceased, they are ruptured and eventually disintegrate. The cortex is ruptured first and carries the epidermis with it. At the same time the endodermis loses its dense protoplasmic content, which causes the Casparian strips to be readily distinguished. The endodermis then sloughs centrifugal to the oil ducts but persists opposite the phloem for a short time, so that the formation of periderm is retarded. When the endodermis finally disintegrates, a shallow groove has been formed (fig. 32).

The pericycle divides rapidly in developing the periderm, and the pericylic oil ducts are separated by constantly increasing intervening cells, and appear at regular intervals about the periphery just inside the cork. They are readily distinguished because of the limited number of epithelial cells, which gradually lose their protoplasm and dis-



Figs. 32–44.—Fig. 32, transverse section of root showing tissues in early stage of secondary growth after disintegration of epidermis, cortex, and endodermis, ×160; figs. 33–41, disintegration of primary xylem (33, diarch xylem plate with protoxylem intact and parenchyma cells before much increase in size, ×220; 34, xylem parenchyma cells increased in size and protoxylem disintegrating, ×110; 35, parenchyma cells wedging between metaxylem, ×110; 36, disintegration and separation of metaxylem by parenchyma, ×110; 37–39, increase in size of parenchyma cells and separation and disintegration of metaxylem and protoxylem, the latter hardly distinguishable in 38 and 39, ×110; 40, all xylem separated by parenchyma, ×110; 41, transverse section of xylem at center of root in which primary xylem is no longer distinguishable and secondary cells are being separated by parenchyma, ×110); fig. 42, transverse section of secondary phloem showing separation of fibers by parenchyma, × 220; fig. 43, transverse section of young bundle, ×220; fig. 44, transverse section of older bundle, ×220 (*c*, cambium; *cr*, cork; *dc*, disintegrating cells; *mx*, metaxylem; *o*, oil duct; *pf*, phloem fibers; *ppa*, phloem parenchyma; *px*, protoxylem point; *sp*, secondary phloem; *sx*, secondary xylem; *x*, xylem; *xpa*, xylem parenchyma).

appear. The secondary phloem is largely composed of parenchyma with scattered groups of phloem and fibers. Immediately after disintegration of the outer tissues, the primary and early secondary phloem groups may be seen 180° apart and located near the periderm; but the rapid growth of the parenchyma continually forces the cells outward and separates them into strands and later into small groups of cells so that they soon become indistinguishable. The phloem parenchyma is much more abundant than the xylem and all of its cells are filled with minute starch grains. Growth appears to be due not to cell division but to enlargement of the individual cells, and it constitutes the greater portion of the mature root, being from ten to thirty times as large as the xylem (fig. 42).

The secondary xylem is differentiated in the form of uniseriate or biseriate (rarely triseriate) rays with constantly widening intervening bands of parenchyma, two of which are unusually broad and lie on the same diameter with the primary xylem. The vessels of the rays and the fibers are gradually separated by the parenchyma, since the cells of the latter increase greatly in size as the root grows older and the very early secondary xylem loses all semblance to ray arrangement, appearing in transverse section as a relatively large circular area at the center of the root with the vessels scattered through the parenchyma; while that which is differentiated later retains the ray formation with single vessels or in strands of from two to six cells and separated by the parenchyma.

Secondary thickening in the permanent lateral roots is similar to that of the primary, but proliferation of the tissues is not so extensive and the cells remain relatively small while lignification occurs early in ontogeny.

Disintegration of primary xylem

The primary xylem remains at the center of the stele for a short time after the outer tissues have sloughed, then the parenchyma cells which separate it from the secondary xylem and which were differentiated in a narrow zone between them increase in size, causing a much wider separation. Concomitantly the vasicentric parenchyma cells increase in magnitude and wedge between the cells of the primary xylem. The protoxylem points are the first to be af-

fected by this pressure, for the walls lose their rigidity and are soon seen in various stages of disintegration (figs. 33–37). They finally disappear, for no trace of them is found in either transverse or longitudinal section and they are apparently resorbed (figs. 38–41). The metaxylem cells are separated into groups and then individual cells, and eventually are scattered in the circular central area where they cannot readily be distinguished from the early secondary vessels (figs. 40–41). In the hypocotyl the pith separates the two archs of the primary xylem plate and the primary and early secondary cells appear scattered in a circular band about it. In the root tip there is little proliferation of parenchyma because lignification begins early and consequently the diarch primary xylem plate remains intact.

Summary

1. The mature root of the parsnip represents the true primary root together with the hypocotyl. A longitudinal section shows that the major portion is composed of phloem parenchyma whose cells are filled with starch grains. The central portion of the root is occupied by a core of xylem, and in the hypocotyl pith lies within the xylem. Coarse leaves are diverged from the foreshortened stem during the first year and a coarse columnar axis bearing leaves, flowers, and fruit is developed during the second year.

2. The primary tissues of the root consist of xylem differentiated as a diarch and two groups of phloem radially arranged and separated by interstitial parenchyma, also a pericycle, endodermis, cortex, and epidermis. The hypocotyl consists of the same tissues except that pith is differentiated at the center and separates the xylem.

3. Oil ducts are differentiated in the pericycle and primary phloem, and are relatively ephemeral.

4. A very small number of plants appeared in which the hypocotyl seemed to be triarch and in which triple cotyledons were developed, but it was determined that the third arch resulted from the splitting of one of the bundles while in transition; and since the associated roots were diarch in every case and various irregularities in structure were noted in each of these plants, they cannot be considered true triarchs.

5. Permanent and transient secondary roots are initiated in the

pericycle, and other groups of laterals are differentiated in the phellogen near the free conductive tissue of transients which have sloughed off.

6. The foreshortened stem differs little in structure from the hypocotyl, except that the pith is broader and the leaf traces form a band of bundles.

7. The transition commences in the lower part of the hypocotyl, and the bundles have been reoriented to a tangential position (or 90° from the original central position) at the level where the cotyledons diverge from the stem and the reorientation from tangential to true endarch occurs in the petiole of the cotyledons. Lateral cotyledonary traces accompany the transition bundles above the cotyledonary plate.

8. The large coarse leaves vary greatly in texture, color, and the number of leaflets involved. The petiole consists of an epidermis, collenchyma, photosynthetic and cortical parenchyma, and bundles which are normally collateral but which separate, reorient, and anastomose frequently, and in these processes various types of bundles are evolved. The blade is composed of an epidermis whose cells are of two types, tabular and tortuous, also palisade cells and spongy mesophyll.

9. Hairs and striations are developed on the ridges of the petiole and floral axis, and on the veins of leaves. Stomata appear on the stem, in the grooves of the petiole and axis and tortuous cells of the leaves.

10. The floral axis is initiated during the first year and develops rapidly during the second. It consists of an epidermis, collenchyma, photosynthetic and cortical parenchyma, a band of bundles, and a central pith which develops a schizogenous split at the internodes. Flowers and fruit develop during the second year.

11. Secondary thickening involves the activity of a cambium, and in the root and hypocotyl the tissues centripetal to the pericycle are sloughed off soon after secondary growth commences and a very regular periderm is developed by the proliferation of pericyclic cells. In the other organs much of the growth is due to cell enlargement, although in the bundles there is a limited amount of cambial activity.

12. The greater portion of the root and hypocotyl remains in a parenchymatous state during the first year, and increase in size is accomplished through the enlargement of individual cells. The primary xylem cells are forced apart by the growth of the xylem parenchyma and the protoxylem is gradually resorbed, while the metaxylem is scattered through the parenchyma and early secondary xylem, from which it is practically indistinguishable.

CHICAGO, ILLINOIS

LITERATURE CITED

1. BARY, A. DE., Comparative anatomy of the phanerogams and ferns. 1884.
2. BLANCHARD, J., The nettle hairs of the parsnip. Revue Horticole. No. 13. **66**:427–428. 1894.
3. COURCHET, M., Étude anatomique sur les Ombellifères. Ann. Sci. Nat. Series 6. **17**:107–129. 1884.
4. EAMES, A. J., and MACDANIELS, L. H., Introduction to plant anatomy. McGraw-Hill, New York. 1925.
5. HILL, T. C., Seedling structure in Piperaceae. New Phytol. **3**:46–48. 1904.
6. HOAR, C. S., A comparison of the stem anatomy of the cohort Umbelliflorae. Ann. Bot. **29**:55–62. 1915.
7. HOFFMAN, H., Ueber die Wurzeln der Doldengewächse. Flora **42**:659–661. 1848.
8. TRECUL, A., Des vaisseaux propres dans les Ombellifères. Ann. Sci. Nat. Series 5. **5**:292. 1866.
9. VAN TIEGHEM, PH., Canaux secreteurs des plantes. Ann. Sci. Nat. Series 7. **8**:22–26. 1888.
10. VAN TIEGHEM, Ph., and DOULIOT, H., Origine des radicelles des dicotylédones. Ann. Sci. Nat. Series 7. **8**:216–219. 1888.

LEADER, NEEDLE, CAMBIAL, AND ROOT GROWTH OF CERTAIN CONIFERS AND THEIR INTERRELATIONS

RAYMOND KIENHOLZ

(WITH FIVE FIGURES)

Introduction

The interrelation between the vegetative and reproductive activities of various plants has been investigated extensively of recent years, but relatively little is known regarding the interrelation between the various growth activities and growth regions of perennial plants, particularly forest trees. Most of the work which has been done deals with the activity of a single or at most two growing regions. Leader elongation and cambial growth have been most frequently investigated, but only rarely have measurements of both of these growth activities been at all consistently recorded for the same species or individual under observation. There seems need, therefore, for measurements of the growth of shoots, leaves, cambium, and roots of the same individual or the same species during the same growing season. Research carried out at the Yale Demonstration and Research Forest near Keene in southern New Hampshire over a period of several years gives a fairly clear, coordinated picture of the interrelation between the several growth activities of red pine and white pine.

During the summer of 1931, the writer measured at weekly intervals the growth of the leader, needles, and cambium of red pine, the leader and needles of white pine, and the leader of several other species of conifers. These data will be discussed together with data on root growth supplied by the work of C. L. STEVENS (24).

The growth of the leader has been much investigated, particularly in relation to meteorological conditions. For a discussion of this work reference is made to the recent article by BALDWIN (1) and to résumés by ROMELL, BURGER, and HERTZ cited by BALDWIN. Only the literature dealing with certain specific phases of tree growth will be discussed in this paper.

MATERIALS USED.—The various groups of conifers observed and measured were all located in the Yale Forest. This forest has been described by TOUMEY (**27**) and need not be discussed here. A group of red and white pines located in one of the plantations was arbitrarily selected as the standard for each species. Other groups of red and white pines of different ages and growing on different sites were measured and compared with the standard. A few other species were included for comparison. The material used is summarized in table I.

TABLE I

DESCRIPTION OF TREES MEASURED

SPECIES	NUMBER USED	AGE	HEIGHT (FEET)	DIAMETER AT 1 FOOT (INCHES)	SPACING
Red pine	12	9	4.9	1.3	4×4
White pine	10	10	4.0	0.9	6×6
Pitch pine	11	Vol.*	5.8	1.6	Irregular
White spruce	20	10	4.0	1.0	6×6
Balsam fir	5	Vol.*	15.0	3.7	Irregular

* Volunteer trees, age unknown.

The soil was in all cases a fine sand, increasing to coarse sand and gravel at lower depths, and with a small admixture of humus in the upper layers. The better sites had a slightly finer, heavier soil with more humus material.

If the curves of leader elongation obtained by C. L. STEVENS (**24**) in 1928 and 1929, and those obtained by R. D. STEVENS (**25**) in 1929, are compared with those obtained by the writer, it will be seen that the time of beginning and ending of leader elongation varies but slightly, while the time of most rapid elongation falls within a few days of June 10 in every case. From this it would appear that the course of leader growth varies but little from year to year. Furthermore, climatic conditions which would hasten or delay one of the growth activities would probably have a similar effect on the others, hence the interrelation between the various growth activities would not be greatly altered from year to year.

The species studied were red pine (*Pinus resinosa* Sol.), white

pine (*P. strobus* L.), pitch pine (*P. rigida* Miller), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Miller).

Results

Leader elongation

The elongation of the leader was measured at weekly intervals during the growing season by means of a measuring device consisting of a triangular head sliding on a graduated blade which rested on a brass nail driven into the older part of the main axis (**12**).

Red pine.—In the standard trees the leader began to elongate late in April, increased rapidly to a maximum rate of 16.1 mm. per day during the week ending June 10, and decreased rapidly and then gradually until growth ceased about August 15, a period of about 104 days (table II, fig. 1). The exact time of beginning and ending of leader elongation is difficult to determine because of the slow and intermittent swelling of the bud in the spring and the formation of the new terminal bud in late summer, which last is not properly elongation of the season's leader. The period of most rapid growth was distinctly marked, however, and extended roughly from May 15 to July 15 (60 days), during which time 96 per cent of the total growth of the season occurred.

Another group of eleven red pines had essentially the same seasonal course of growth as the standard trees. Five red pines, 6 years older than the standard trees, began and ended growth slightly later than the standard trees and reached their maximum growth rate June 17 instead of June 10. The slight difference may be due to the greater sluggishness of the older trees.

A group of seven red pines began and ended their leader elongation sooner than the standards and reached their maximum rate June 2 instead of June 10. The earliness of these trees compared with the standard trees was probably due to the fact that they were located on a southwest slope where air drainage was better and spring air temperature higher than for the checks. The mean air temperature in this group for the first two weeks of May was 54° compared with 52° F. for the standards.

TABLE II

MEAN DAILY ELONGATION OF LEADER SHOOT (IN MM.)

SPECIES	NO. USED	MAY 1	MAY 6	MAY 13	MAY 20	MAY 27	JUNE 3	JUNE 10	JUNE 17	JUNE 24	JULY 1	JULY 8	JULY 15	JULY 22	AUG. 5	AUG. 18
Red pine	12	.....	1.0	1.7	3.5	5.7	15.1	16.1	13.1	9.2	6.7	1.4	1.0	0.9	.....	0.1
White pine	10	.....	.....	1.2	2.2	3.6	7.2	10.0	8.6	6.4	6.0	4.8	2.5	0.6	0.1	0.1
Pitch pine	11	.....	.....	1.2	2.4	5.0	12.6	14.7	12.3	5.1	2.3	0.5	1.5	0.4	0.4	.....
White spruce	20	.....	.....	.....	1.2	2.8	7.8	10.7	7.5	7.1	5.0	1.9	0.2	0	0	.....
Balsam fir	5	.....	.....	.....	0	2.4	4.2	5.5	6.6	6.8	5.2	3.4	2.4	0	0	.....

WHITE PINE.—Leader elongation in the white pine standard trees started slightly later than in the red pines, but reached its maximum rate at the same time (June 10) and ceased growth at the same time. The maximum growth rate was 10.0 mm. per day compared with 16.1 mm. for red pine. Most of the growth (96 per cent) occurred, as in red pine, from May 15 to July 15.

A group of five older white pines began and ended growth later but reached their maximum rate at the same time as the standards. This behavior is somewhat similar to that of the older red pines.

A group of four white pines located on a southwest facing slope had a seasonal course of elongation similar to that of the red pine grown under similar conditions; that is, they began and ended growth earlier than the standard trees and reached their maximum June 2 instead of June 10.

PITCH PINE.—Leader elongation began about the same time as in white pine, increased rapidly to a maximum of 14.7 mm. per day (June 10), and fell off rapidly by early July. An increased elongation occurred July 15 owing to the formation of a very long bud characteristic of this species. It had completed 97 per cent of its total growth for the season from May 15 to July 15 (60 days).

WHITE SPRUCE.—Leader elongation had barely started by May 13, but

increased rapidly to a maximum rate of 10.7 mm. per day the week ending June 10, and ceased growth July 23. It was possible to determine more accurately when leader elongation began and ended in spruce than in red and white pine. Practically the entire leader elongation took place from May 15 to June 15.

BALSAM FIR.—No elongation occurred before May 20, but by May 27 the leader was growing rapidly. Leader growth increased to

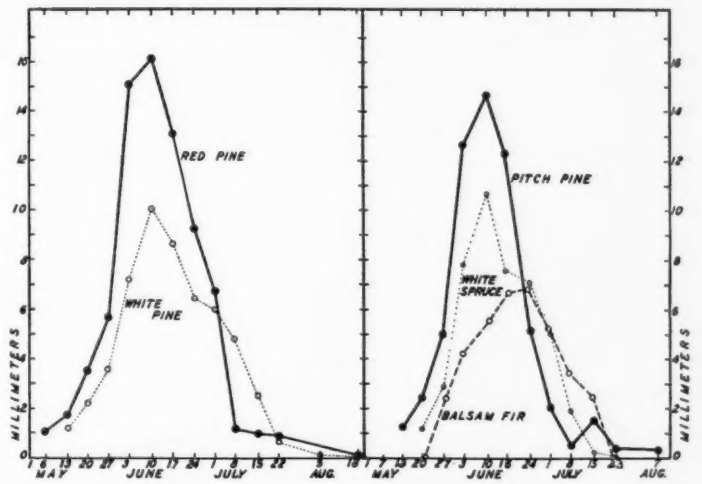


FIG. 1.—Seasonal course of leader elongation in several species of conifers (daily increment by weekly periods in mm.).

a maximum rate of 6.8 mm. per day on June 23, two weeks later than in the other species. It ceased July 23. Balsam fir has a short growing season, starting later and ending earlier than the other species studied. It practically completed its growth in 65 days as compared with about 105 days for red, white, and pitch pine and 70 days for white spruce.

With the exception of balsam fir, all the species studied reached their peak June 10. Red pine started growth earliest, followed closely in order by white pine, pitch pine, white spruce, and balsam fir, with little difference between the first three species. Growth ceased about the same time in the three species of pines. Spruce and fir

ceased growth slightly earlier than the pines. Balsam fir had a very abrupt beginning and ending of leader elongation; spruce less so; while the pines began and ended growth gradually, probably owing to the way in which their terminal buds swelled in the spring and formed in the later summer.

DAY AND NIGHT ELONGATION OF THE LEADER

For a period of 17 days (June 13–29) the leader elongation of the twelve check red pines was recorded every morning and evening at 6:30. This divided the day into halves corresponding rather closely to the periods of daylight and dark and their corresponding temperature changes. Within a few feet of the trees the temperature of the air was recorded by a hygrothermograph and by standard Weather Bureau maximum and minimum thermometers installed in louvered shelters.

With the exception of two days, June 24 and 25, the amount of growth occurring during the night was greater than that occurring during the day (fig. 2). The average increment for the 17 days was night growth 5.93 mm. and day growth 4.47 mm., or in the ratio of 100 to 75. ILLICK (**10**) reports a similar increase of night growth over day growth for a number of trees; for white pine the ratio was 100 to 70.

When the minimum and maximum temperatures were compared with the amounts of day and night growth, a fair degree of correlation was found to exist between night growth and minimum temperature ($+0.744 \pm .075$) and between night growth and mean temperature ($+0.747 \pm .075$). On cold nights when the temperature dropped to 42° or lower, the amount of growth was very slight while on warm nights the growth was greater. During the two times when day growth surpassed night growth the minimum temperatures were low, being 42° and 34° respectively. The correlation between night growth and maximum temperature of the day before was not statistically significant. There was likewise no significant correlation between day growth and temperature. Saturation deficit was probably more important than temperature in determining the amount of growth per day (**20**), but no data are available on this point.

The data on night growth show the dependence of growth on temperature, and particularly the retarding effect of cold nights. It seems likely that early in the season (because of colder nights) the amount of growth at night would be less than during the day, as has been shown by TOLSKY (**26**) for southern Russia.

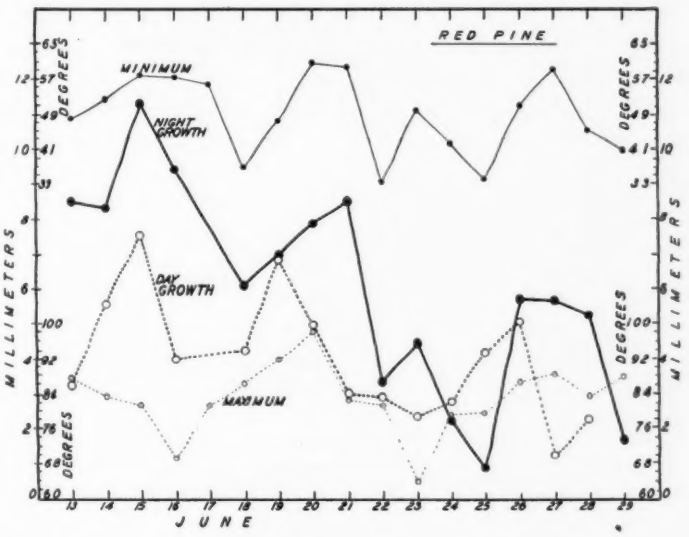


FIG. 2.—Day and night elongation of the leader of red pine in relation to temperature (increment in mm.).

NEEDLE ELONGATION

Four needles on the south side and four needles on the north side of each leader were measured at weekly intervals during the growing season. These needles were located on the base, lower middle, upper middle, and tip portions of the leader. Each fascicle in pine is subtended by a bract, the lower part of which is firm and persistent and the upper part of which is chaffy and deciduous. The persistent base of the bract served as an unvarying zero point from which to measure the growth of the needles, particularly when young. When older the celluloid millimeter ruler was slipped between the needle and the twig. In the case of red pine the two needles of the fascicle were

usually the same length, while in white pine the five needles of the fascicle varied somewhat. Their average length was measured in each case. The eight chosen fascicles were marked at their bases with black India ink and the same needles were remeasured each time unless injured, in which case they were discarded.

In order not to injure the delicate underlying needle primordia nor to retard needles or leader growth by too early exposure to drying, the chaffy scales were removed by hand after the needles had already put on some growth. This was particularly true of the basal needles, hence their curve of growth is incomplete. The needles at the tip of the leader, however, were not yet visible above the base when observations began, hence data covering their entire growth period were obtained. There was practically no difference between the growth of the needles on the north and south sides of the leader, hence they were averaged together.

When the growth of the basal needles was compared with that of the needles located higher on the leader a distinct progression was noticed. That is, in the case of the standard red pines the basal needles were 9.4 mm. long on June 1, were growing vigorously on June 12, had reached their maximum growth rate on June 24, and decreased gradually to August 19 (fig. 3). The tip needles on the other hand were not yet visible above the bract base on June 1, but had begun growth by June 12. They reached their maximum growth rate on July 8, two weeks later than the basal needles, and then fell off gradually to cease growth by September 2. The lower middle and upper middle needles followed courses of growth intermediate between those of the basal and tip needles. A wave of growth progresses from the base of the leader to its tip, which causes each needle to pass through its grand period of growth earlier than those above it. Although this progression is marked in the time of starting and the time of reaching the maximum, it is not so marked in the time of ending growth (fig. 3).

In each of the 65 red, white, and pitch pines investigated, the growth of the needles showed the same progression of development from the base to the tip of the leader already described for red pine. However, the difference between the base and tip needles was not so great in white and pitch pine as it was in red pine.

More accurately to indicate the seasonal course of growth of the needles over the entire leader, the eight needles from each tree were averaged together for the trees of the group, thus reducing needle growth to a single curve.

RED PINE.—Because of the danger of damage to the delicate meristematic tissues at the base of the needles the early growth of the basal needles was not obtained, hence the total growing period of the

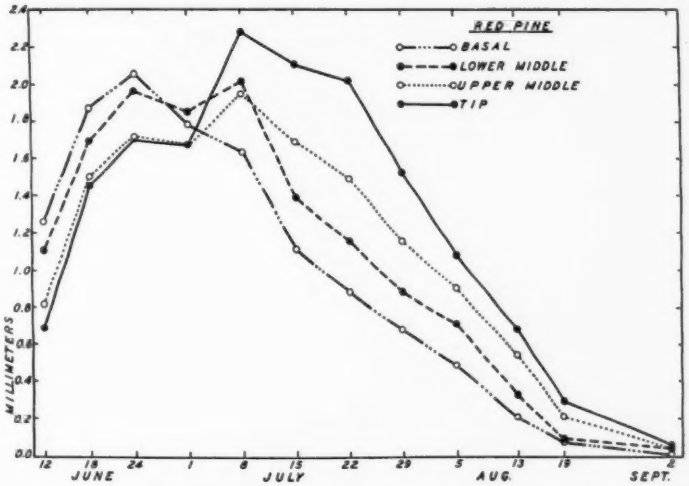


FIG. 3.—Seasonal course of elongation of red pine needles located at different levels on the leader (daily increment by weekly periods in mm.).

needles is only approximately known. But by knowing the length of the basal needles at the time of first measurement (June 1), it can be determined that they started growth about May 15. The tip needles were not showing above the bract base on June 1, but averaged 9 mm. long on June 12; hence they must have started growth shortly after June 1. They grew until September 2, a growing period of 94 days. The basal needles grew from about May 15 to early September, so that the entire time during which needle elongation occurred was about 110 days (table III, fig. 4). Most of the growth (94 per cent) occurred between June 10 and August 10 (60 days).

A comparison of needle elongation showed little difference be-

TABLE III

MEAN DAILY ELONGATION OF NEEDLES (IN MM.)

Species	No. of needles	Initial length, June 2	June 12	June 18	June 24	July 1	July 8	July 15	July 22	July 29	Aug. 5	Aug. 13	Aug. 19	Sept. 2
Red pine	268	3.4	1.03	1.63	1.86	1.74	1.96	1.54	1.39	1.06	0.80	0.44	0.17	0.03
White pine	144	4.2	0.55	0.90	0.98	1.08	1.32	1.34	1.10	0.85	0.54	0.17	0.08	0.02
Pitch pine	72	4.2	0.80	1.12	1.42	1.24	.....	1.34	0.94	0.70	0.53	0.34	0.30	0.04

tween various groups of red pine trees. There was a tendency, however, for the older trees to start and end growth later than those trees located on the southwest slope, a behavior similar to that noted for leader elongation in these same groups.

WHITE PINE.—Needle elongation started at about the same time as in red pine but ceased slightly earlier. The maximum growth rate was reached about a week later than in red pine. There was very little difference between the different groups of white pine.

PITCH PINE.—The seasonal course of needle elongation was similar in pitch pine and red pine, although the amount of growth was less in pitch pine than in red pine.

An examination of needle elongation showed that nearly every needle measured decreased its rate of elongation during the week ending June 30 as compared with the weeks before and after. Because of this lessened growth rate the curve of needle elongation, particularly in red pine, showed a dip on June 30 with a rise on either side (in other words, a double maximum). Such a curve is unusual, particularly with the two maxima only two weeks apart. The peculiar shape of the curve was not due to a small number of samples since the same dip in the curve was obtained by plotting the mean of more than 250 needles. The fact that nearly all the needles were retarded in their growth rate pointed to meteoro-

logical conditions as the cause. The air temperatures at a station near the standard red pine trees were as follows:

	JUNE 24	JUNE 30	JULY 8	JULY 16
Mean maximum	82.4	87.3	86.4	85.6
Mean minimum	49.0	45.8	57.2	57.2

The week ending June 30 had the highest maximum air temperature, including one day of 100° and the lowest minimum including one night of 34° F. Moreover, the relative humidity was much lower

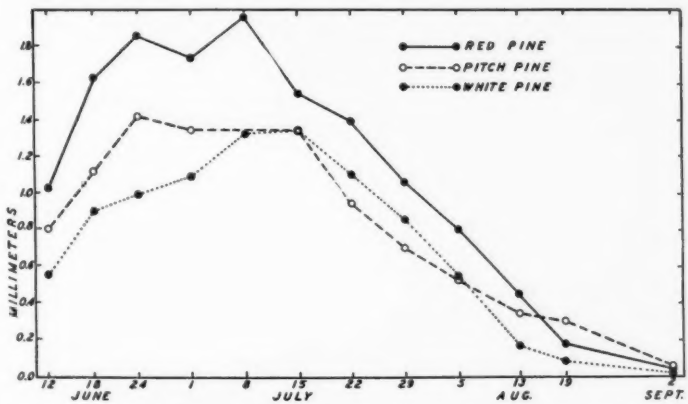


FIG. 4.—Seasonal course of needle elongation in several species of conifers (daily increment by weekly periods in mm.).

during the week ending June 30 than during the following weeks. Meteorological conditions, particularly the cold nights, retarded growth and converted what would probably have been a maximum growth rate into one slightly lower than that of the preceding and succeeding weeks.

GROWING REGION OF NEEDLES

In late July a number of needles of red, white, and pitch pine were marked into 2 mm. intervals by means of India ink lines and later remeasured at intervals. In every case all elongation took place at the extreme base of the needle within the protective basal sheath; that portion of the needle above the sheath showed no signs of further elongation. In white pine, the distinct scales of which the

sheath is composed also elongated at their bases. BÜSGEN (**3**) states that after the first rapid elongation of the young needles, growth proceeds from an active zone at the base.

DO THE NEEDLES GROW FOR MORE THAN ONE YEAR?

Considerable controversy has arisen in the past over whether or not the needles of pine grow in length after the first year. KRAUS (**14**) maintained that they did, while MEISSNER (**19**) insisted that they did not. HONDA (**7**), working with *Pinus longifolia* in Japan, found the needles did not grow in length the second year. More recently HAASIS (**5**) reported elongation after the first year in the needles of Monterey pine defoliated in March, while LODEWICK (**16**) reported increased length during their second year for the needles of longleaf pine in Florida.

A great number of needles measured in September, 1930, were remeasured in May and October, 1931. These needles were from both red and white pine trees of different ages, growing in the open or in the shade, and from trees defoliated or not defoliated. In no case was there any elongation the second year. Apparently elongation the second year is a matter of species difference and geographical location, with such factors as defoliation also of some importance.

DAILY NEEDLE ELONGATION

Four needles on each of the twelve standard red pine trees were measured daily at about 8 A.M. for a period of 24 days (June 30 to July 23) and the mean daily growth rate determined. A comparison of the rate of elongation for each day with the mean temperature for the same period showed a positive correlation of $+0.627 \pm 0.08$. This correlation was particularly evident when growth was very rapid or very slow. The maximum temperature showed a correlation of $+0.618 \pm 0.08$ with the growth rate, while the minimum temperature showed no significant correlation.

GROWTH OF CAMBIUM

Dendrographs of the type devised by MACDOUGAL (**18**) were attached to two red pine trees at about 1 foot above the ground. One of these trees grew in an open 8×8 plantation and was 18 feet high and 6.1 inches in diameter at a height of 1 foot. The other tree grew

near by, partly under a canopy of gray birch and poplar. It was but slightly affected by this competition, however, since it was 16 feet high and 4 inches in diameter at a height of 1 foot. The two records were almost identical, hence their average is here presented.

No growth had taken place by May 5, but by May 12 growth had begun and increased rapidly to a first maximum on June 2, decreasing slightly to increase to a second maximum on July 9. Growth gradually became less and less, ceasing about October 1, a growing period of 150 days. The records of both trees agreed in having their maxima on June 2 and July 9. There was no correlation between the maximum, minimum, or mean air temperatures and the average weekly growth rate, nor between the relative humidity and the growth rate; hence it would seem that the double maximum was not due to climatic conditions but to some internal factor.

The literature on diameter growth of trees shows a number of instances recorded by BROWN (**2**), FRIEDRICH (**4**), JOST (**11**), and LODEWICK (**15**) in which there was a flattening of the curve of growth, presumably at the time of transition between spring wood and summer wood formation. Although no histological examination of the tissues was made in this study, the similarity between the results here recorded and those based on periodic microscopic examination of the cambial region (**15**) points strongly to the view that the first maximum (June 2) was due to spring wood formation and the second maximum (July 9) to summer wood formation.

ELONGATION OF ROOTS

No data are available on the root growth of red pine, hence the following data are taken from the work of STEVENS (**24**, table VII and plate VI) on white pine in 1929. Elongation of the roots of white pine began about the middle of April, reached a first maximum June 8, dropped off to a low growth rate August 3, rose again to a second higher maximum on October 4, and fell off to cease growth in early November, a growing period of about 205 days (fig. 5).

INTERRELATION OF GROWTH ACTIVITIES

When leader elongation, needle elongation, cambial growth, and root elongation are compared with one another (fig. 5), an interrelation can be seen between the various growth activities and growing

regions of the tree. Since each growing region draws water, mineral nutrients, and elaborated foods to itself, there must be a constant and probably severe competition for these growth materials which are usually limited in amount. As one growing region increases in activity the attraction it exerts on available growth materials becomes greater (3). This decreases the supply available to some other growing region, which may gradually cease its activities through lack of materials (21). What normally causes beginning and cessa-

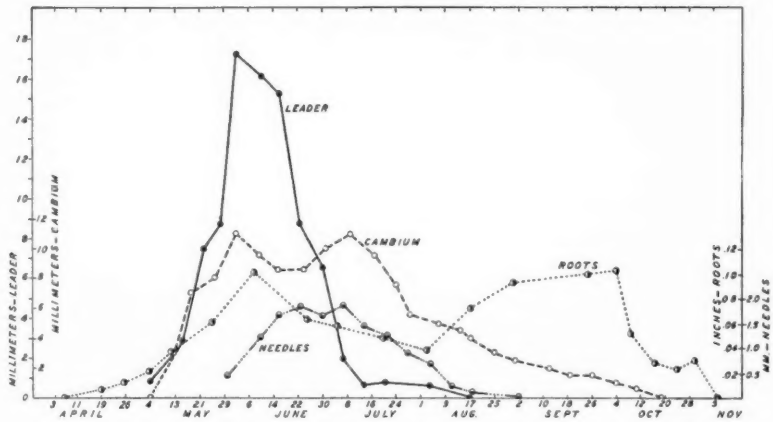


FIG. 5.—Interrelation of the different growth activities of pine (cambium growth expressed as amount of increase in diameter since previous week's reading; all others, daily increment by weekly periods).

tion of activities in the various growing regions of the tree is not known. In the case of leader elongation at least, it was certainly not low temperature since growth ceased in July or August while the temperatures were still relatively high. Nor is it known what causes the double maximum in the rates of cambium growth and root elongation. It seems probable, however, that the cause is to be sought in an internal balance between the different growth activities of the tree, or, as PRIESTLEY (23) states, "the fluctuation in the internal factors correlating growth, including a fluctuating balance of metabolic activities." And when it is realized that the attraction of a growing region may be primarily for water, or various mineral nutrients,

or different elaborated foods at different times, the process becomes even more complex. The present data and discussion can do little more than throw into relief the various problems arising from the interrelation of all growth activities by presenting what is known concerning a species during a growing season.

The first organ to begin growth was the root, followed by the leader and the cambium, and considerably later by the needles. Although there was a slight amount of early root and leader elongation previously, their rapid growth did not begin until about May 1. After May 1 there was a great surge of growth in the leader, in the roots, and in the cambium at approximately the same time. This extensive activity was probably due to the ready availability of a relatively large amount of stored food and the presence in the wood of an abundance of water. Leader elongation reached a maximum (in those trees to which the dendrographs were attached) at the same time as the first maximum of cambium growth (June 2), followed closely by the first maximum of root elongation (June 8). There is probably a causal relation between these three growth activities of the tree connected with the absorption of water by the elongating roots, its transportation by the newly formed spring wood, and its utilization by the rapidly elongating shoots. The slump in growth rate of the leader and roots and cambium appears to be associated with the depletion of reserve foods stored in the tree.

Needle elongation began while the roots, cambium, and leader were growing rapidly and reached its maximum growth rate when roots, cambium, and leader were decreasing their growth rate. The considerable mass of material needed to develop the current set of needles may well have decreased the food supply to the other growing regions of the tree, causing them to grow more slowly. This would be the case whether the food available were from stored material or from food synthesized by the needles. It is likely that most of the food available at this stage of the development was newly synthesized by the old needles, and would thus be readily available to the newly developing current set of needles, since nearness to the supply often determines which organ receives the greater amount of food (17). As these needles become more active photosynthetically through greater surface, they would increasingly make food avail-

able for the second surge of growth of the cambium (July 9). This growth, at first largely cell extension, would be followed by differentiation and maturation of the thick walled, late summer wood cells requiring large amounts of carbohydrates. Late wood cell differentiation might well occur in early August, since BROWN (2) states that late wood formation in white pine begins during the first half of August and is associated with a decrease in growth intensity. Thus the greatest utilization of food by the cambium would occur when most of the other growing regions of the tree were growing relatively slowly, and might account for the decreasing growth rate of the needles and roots.

The behavior of the roots with their greatly reduced elongation during early August is most striking. This decrease in rate of elongation of the roots may be due to the diversion of foods to the differentiating late wood cells as already suggested, or it may be due to the balance between radial growth and elongation in the root itself. Few data are available as to just when radial growth takes place in the roots, but HARTIG (6) believes that it starts late in the season (August). PETERSEN (22) maintains that the midsummer period of decreased root elongation is correlated with maximum radial growth in the older roots.

With a full complement of needles functioning during August and September, food is being produced in abundance, which may result in carbohydrate accumulation. Some of this food is transported to the roots and probably accounts for the increased elongation of the roots in early October, since HOOKER (8) states that roots use carbohydrates; hence an accumulation of carbohydrates in the aerial parts of the plant, which may cause them to cease growth, tends rather to favor root growth. What causes cambial development to cease is not known, although by late September temperature may be a limiting factor. PRIESTLEY (23) suggests that the replacement of sap by air in the tracheids near the cambium may bring about a deficiency of water and cause the cambium to cease functioning. HOWARD (9) suggests that an accumulation of carbohydrates which checks enzyme action brings about the rest period. Root elongation is probably stopped by low temperature.

Thus aside from the first surge of growth during which the leader

reaches a maximum and the roots and cambium reach a first maximum growth rate at nearly the same time, the growth activities of the tree reach their maxima at different times in the order: needles, cambium, and roots. After the store of reserve food has been largely depleted, the interrelation between the various growth activities of the tree seems to be dependent upon the availability of food, water, and possibly mineral nutrients.

A similar correlation between the various growing organs of the cotton plant is suggested by the work of BALLS and HOLTON as analyzed and presented graphically by PEARSALL (**21**). In cotton, growth of the stem apex was decreased by the growth of large numbers of flowers whose growth was in turn decreased by growth of the fruit. PEARSALL (**21**) shows a falling off in the rate of elongation of the main root of peas and beans at the time of secondary root production, and increased growth following the removal of the shoot. KNY (**13**) and TOWNSEND (**28**) note an increase in the rate of growth in roots following removal of shoots. Such results must always be considered in the light of the amount and the place of storage of food available for growth.

Summary

1. The seasonal course of leader elongation, needle elongation, and cambial growth of certain conifers, particularly red pine and white pine, was measured during the 1931 growing season near Keene, New Hampshire.

2. Leader elongation in red pine began in late April, reached its maximum by June 10, and ceased about the middle of August, a growing period of approximately 105 days. Ninety-six per cent of this growth was made during the 60 day period from May 15 to July 15. Older trees were slightly later in their seasonal course of leader elongation than were younger trees. Trees located on southwest slopes started growth earlier than those located on level areas.

3. Leader elongation in white pine started slightly later than in red pine but reached its maximum at the same time (June 10) and ceased growth at the same time. Ninety-six per cent of the growth occurred from May 15 to July 15.

4. Leader elongation in pitch pine followed a seasonal course

similar to that of white pine. Ninety-seven per cent of this growth occurred from May 15 to July 15.

5. Leader elongation in white spruce started the middle of May, reached a maximum June 10, and ceased July 23, a growing period of about 70 days.

6. Leader elongation in balsam fir started late in May, reached a maximum June 23 (two weeks later than the other species), and ceased July 23, a growing period of about 65 days.

7. From June 13 to June 29, 60 per cent of the leader elongation of red pine occurred at night, 40 per cent during the day. A correlation of $+0.744 \pm 0.075$ existed between night growth and minimum temperature. No significant correlation existed between day growth and temperature.

8. The needles located at the base of the leader in red, white, or pitch pine pass through their grand period of growth earlier than do those located higher up on the leader. Those at the tip began elongation about June 5.

9. Needle elongation in red pine began about May 15, reached a maximum late in June, and ceased in early September, a growing period of 110 days. Ninety-four per cent of the growth occurred during the 60 days from June 10 to August 10.

10. Needle elongation in pitch pine was similar to that of red pine; white pine was slightly more tardy in its development than red pine.

11. Needles of the pines investigated grow from a meristematic region at their base. They do not elongate after the first growing season.

12. Daily needle elongation in red pine showed a correlation of $+0.627 \pm 0.08$ with the mean temperature.

13. Cambial growth in red pine as measured by the MacDougal dendrograph began in early May, reached a first maximum June 2, decreased slightly and reached a second maximum July 9. Growth ceased in early October, a growing period of 150 days. There was no correlation between the meteorological conditions and the double maximum in the growth rate. The first maximum is probably associated with the development of spring wood and the second maximum with the development of summer wood.

14. STEVENS reports that the roots of white pine begin to elongate the middle of April, reach a first maximum June 8, decrease, rise to a second maximum on October 4, and cease in early November, a growing period of about 205 days.

15. There is a certain interrelation between the activity of the different growing regions of the tree. In early June there is a great surge of growth in leader, roots, and cambium at approximately the same time. This spurt of growth is made possible by the great amount of readily available reserve foods stored in the tree. There is probably a causal relation between these different growth activities having to do with the absorption, transportation, and utilization of water.

16. After this first surge of growth the needles reach their maximum growth rate, followed by the second maximum of cambial growth. After nearly all growth is completed and the full complement of needles is functioning, the roots reach their second maximum rate of elongation.

17. It is suggested that there is an internal balance between the metabolic activities of the different growing regions of the plant which determines the time of maximum development of needles, cambium (late wood formation), and roots. After the reserve foods are exhausted this balance is necessitated by limited supplies of elaborated foods, water, and possibly mineral nutrients.

AGRICULTURAL EXPERIMENT STATION
NEW HAVEN, CONNECTICUT

LITERATURE CITED

1. BALDWIN, H. I., The period of height growth in some northeastern conifers. Ecology **12**:665–689. 1931.
2. BROWN, H. P., Growth studies in forest trees. II. *Pinus strobus* L. BOT. GAZ. **59**:197–241. 1915.
3. BÜSGEN, M., and MÜNCH, E., The structure and life of forest trees. Transl. by T. THOMSON. Wiley & Sons, New York. 1931.
4. FRIEDRICH, J., Über den Einfluss der Witterung auf den Baumzuwachs. Mitt. Forstl. Versuchs. Oester. **22**:1–160. 1897.
5. HAASIS, F. W., Notes on the growth period of Monterey pine leaves. Bull. Ecol. Soc. Amer. **12**. 1931.
6. HARTIG, TH., Über die Zeit des Zuwachses der Baumwurzeln. Bot. Zeitschr. **21**:288–289. 1863.

7. HONDA, S., Besitzen die Kiefernadeln ein mehrjähriges Wachstum? Imp. Univ. Coll. Agr. Bull. **2**:391–392. 1896.
8. HOOKER, H. D., The physiological significance of carbohydrate accumulation. Proc. Int. Cong. Plant Sci. Ithaca, New York (1926). **2**:1071–1080. 1929.
9. HOWARD, W. L., An experimental study of the rest period in plants. Physiological changes accompanying breaking of the rest period. Missouri Agr. Exp. Sta. Res. Bull. **21**:1–72. 1915.
10. ILLICK, J. S., When trees grow. Amer. For. **25**:1386–1390. 1919.
11. JOST, L., Betrachtungen über den zeitlichen Verlauf des sekundären Dickenwachstums der Bäume. Ber. Deutsch. Bot. Ges. **10**:587–605. 1892.
12. KIENHOLZ, R., A useful instrument for measuring height growth. Plant Physiol. **7**:556–558. 1932.
13. KNY, L., On the correlation in the growth of roots and shoots. Ann. Botany **8**:265–280. 1894.
14. KRAUS, G., Das mehrjährige Wachsen der Kiefernadeln. Abhand. Naturforsch. Ges. Halle **16**:361–372. 1883–1886.
15. LODEWICK, J. E., Seasonal activity of the cambium in some northeastern trees. New York State Coll. For. Tech. Publ. 23. 1928.
16. ———, Some effects of irrigation and fertilization on the size of longleaf pine needles. Forest Worker **7**:12–13. 1931.
17. MASON, J. G., Growth and correlation in sea island cotton. West Indian Bull. **19**:214–238. 1922.
18. MACDOUGAL, D. T., Growth in trees. Carnegie Inst. Wash. Publ. 307. 1921.
19. MEISSNER, R., Studien über das mehrjährige Wachstum der Kiefernadeln. Bot. Zeitschr. **52**:55–82. 1894.
20. NAKASHIMA, H., Über den Einfluss der meteorologischen Faktoren auf den Baumzuwachs. II. Jour. Fac. Agr. Hokkaido Imp. Univ. Sappora, Japan **22**:301–327. 1929.
21. PEARSALL, W. H., Studies in growth. IV. Correlations in development. Ann. Botany **37**:261–275. 1923.
22. PETERSEN, O. G., Nogle Undersøgelser over Traeernes Rodliv. Overs. Kong. Danske Vidensk. Selskab. 1–68. 1898 (cited by PRIESTLEY).
23. PRIESTLEY, J. H., Studies in the physiology of cambial activity. III. The seasonal activity of the cambium. New Phytol. **29**:316–354. 1930.
24. STEVENS, C. L., Root growth of white pine (*Pinus strobus* L.). Yale Univ. School For. Bull. 32. 1931.
25. STEVENS, R. D., Height growth in red and white pine as influenced by weather conditions. In manuscript. 1931.
26. TOLSKY, A. P., Trans. For. Exp. St. Petersburg **47**:1913. in For. Quart. **12**: 277–278. 1914.
27. TOUMEY, J. W., The Yale Demonstration and Research Forest near Keene, N.H. Yale Univ. School For. Bull. 33. 1932.
28. TOWNSEND, C. O., The correlation of growth under the influence of injuries. Ann. Botany **11**:509–532. 1897.

EMBRYOGENY OF CARYA AND JUGLANS, A COMPARATIVE STUDY[1]

LaDema M. Langdon

(WITH PLATE I AND FIFTY-SIX FIGURES)

Introduction

While numerous studies have been reported (Hanstein, 1870, Westermeier, 1876, Hegelmaier, 1878, 1897, Famintzin, 1879, Guignard, 1881, Coulter and Chamberlain, 1903, Schaffner, 1906, Souèges, 1916–1928, and others) dealing with the embryogeny of angiosperms (including representatives of a large number of families of both Dicotyledoneae and Monocotyledoneae), information relating to the embryological development of the woody ament-bearing angiosperms, especially the Juglandaceae and Fagaceae, remains markedly deficient.

Benson's contributions (**2**) were concerned chiefly with pollination and embryo sac phenomena in certain genera of the Betulaceae and Fagaceae. They added little to the true embryogeny of the Amentiferae. Conrad (**7**) contributed a brief description of the development of ovule, archesporial tissue, embryo sac, and endosperm in *Quercus velutina*. Seven lines at the close of his paper are devoted to the embryo.

Benson and Welsford (**3**) described the morphology of the ovule and female flowers of *Juglans regia* and allied genera, with special reference to their vascular structure. Prior to that, the development of the female flowers and pollination in different species of *Juglans* had been dealt with by Nawaschin (**12, 13**), Karsten (**8**), and Nicoloff (**15**). In a comparative study of pollen tube features and the male gametophytes of chalazogamens, Nawaschin and Finn (**14**) have also given considerable attention to the embryo sac and fertilization in *Juglans nigra* and *J. regia;* and on the basis of gametophyte characters determined in the *Juglans* type are inclined to regard the

[1] A section of this report was presented before the General Section of the Botanical Society of America at Atlantic City, December, 1932. The investigation has been aided by grants from the Committee on Grants-in-Aid, National Research Council.

Juglandaceae as survivors of a series of extinct transition forms between the two great seed-plant groups. In this connection, they place special emphasis upon a certain distinctive character of *Juglans*, foreign to other angiosperms, namely, the retention here of the "two kerneled generative cell" or the capsular inclosure of the pair of discharged sperm nuclei.

Of interest, particularly to the horticulturist, are the more recent investigations of STUCKEY (**19**), WOODROOF (**20, 21, 22**), ADRIANCE (**1**), and SHUHART (**16**). STUCKEY has studied certain phases in the development of the pecan flowers, recording for 25 varieties of *Hicoria pecan* data relative to the time of maturity of the pollen and period of receptivity of the pistillate flowers. Fruit bud differentiation and development of the flowers, embryo sac, and fruits of the pecan, with brief reference to embryological characters, appear in a series of papers by J. G. and NAOMI WOODROOF (**20–22**). Their observations concerning the embryogeny of this form may be summarized as follows: The first division of the egg (occurring eight to nine weeks after pollination) is horizontal, forming a chalazal cell and a large one-celled suspensor, the chalazal cell continuing division in such a manner as to produce a round globular embryo attached at the micropylar end of the sac. A 2- to 4-celled embryo is reported ten weeks after pollination, and a 32- to 64-celled embryo eleven to twelve weeks after pollination, with development of the cotyledons within one month of the first division of the egg.

Recently SHUHART (**16**) has made a study of the morphology and anatomy of the fruit of the pecan, giving particular attention to the origin and development of the carpellate inflorescence, differentiation of the floral organs, and the vascular organization of the young fruit. The development of the embryo is treated only briefly, his observations confirming those previously reported by WOODROOF and WOODROOF, except that SHUHART finds the orientation of the cotyledons transverse to the plane of the middle septum of the fruit, as described by DE CANDOLLE (**6**) and NICOLOFF (**15**).

Investigation

Representatives of the Juglandaceae and Fagaceae selected for the studies in progress are *Carya glabra*, *Juglans mandshurica*, *Quercus*

rubra, *Q. alba*, and *Fagus ferruginea*. Pollination and fertilization, with derivation and development of the endosperm, are to be investigated in these forms, but particular attention is given to their embryogeny, especially in its later phases, including details of origin of cotyledons, primary root, and plumular bud, with the morphology of the growing points of root, shoot axis, and foliar organs; that is, an attempt is made to bridge the gap between early embryogeny and early seedling development.

The present report presents, in a comparative form, certain of the observations and conclusions reached in the course of the study, particularly as they relate to the Juglandaceae. For this section of the project, collections of material for imbedding were taken at frequent intervals, from April to August, 1931 and 1932, from trees on the campus and in the arboretum of Johns Hopkins University, and from the gardens of Dr. E. A. ANDREWS at Govans, Maryland. Both in *Carya* and in *Juglans*, samples were secured from swelling buds and tips of growing shoots before the appearance of the carpellate flowers. Following the appearance of the carpellate flowers, early in May, collections were made three to four times weekly to the time of pollination (May 6–10 in *Juglans*, May 12–15 in *Carya*), after pollination daily for a period of two weeks; and then at intervals of two to three days through June, July, and early August (periods of embryo and fruit development).

Approximately 350 fixations of *Carya* and *Juglans* were prepared and imbedded through the two collecting seasons. Fixation of the flowers and fruits has been with formalin-acetic-alcohol or with Bouin's fluid, the latter giving greater satisfaction in fixation of young embryo sacs. To insure the best possible penetration of fixing, clearing, and imbedding agents, the cupule and ovarian wall (exocarp) were trimmed from opposite sides of the ovulate flowers and fruits, either in the plane of or at right angles to the plane of the middle septum. In preparing the older fruits for paraffin imbedding, it was found advisable, after exhausting as much air as possible from the tissues, to substitute in dehydration mixtures of ethyl and n-butyl alcohols for the usual ethyl alcohol-xylene series (**23**). Serial sections, 8–10 μ in thickness, were then secured with a rotary micro-

tome, or when dealing with the more refractory tissues of the older fruits, with a Spencer sliding microtome (**9**).

I. CARYA GLABRA

CARPELLATE FLOWERS.—The morphology of the flowers and ovules of the Juglandaceae has been treated at some length in previous papers (**2, 6, 8, 15, 16, 19, 20**), and will receive further and more detailed consideration in a later comparative study of this series, involving both the Juglandaceae and the Fagaceae.

In *Carya glabra* several female flowers may be differentiated on the floral axis, but only three or four of the basal or first formed continue in development, becoming visible above the leaves of the shoot early in May. The basal flowers of carpellate inflorescences collected early in May (figs. 5, 13)[2] exhibit characteristic floral features with calyx and stigmas well developed, some expansion of the receptacle, and ovule already inclosed by the carpels. The younger apical flowers of the clusters display partially developed calyces and short, lobelike carpels which have not as yet closed above the developing placenta. Under ordinary circumstances these apical flowers of each ovulate head do not reach maturity, but are shed shortly before or directly after pollination. Two, occasionally three, flowers of each cluster reach full development and become receptive.

Stages in ovule development observed in flower heads collected at this period (May 1–5) range from the initiation of the nucellus as a blunt, conical primordium at the tip of the columnar placenta to partially matured ovules with megasporocytes in synizesis or pachytene.

The megasporocyte is readily distinguished in the young ovules of *C. glabra*, even before initiation of the integument, as a slightly enlarged cell (the nucleus in one of the pre-synizetic phases) lying fifth or sixth in an axial strand of the nucellus. WOODROOF (**22**) and SHUHART (**16**) likewise report the presence of a definitely differentiated megaspore mother cell in the pecan, and NAWASCHIN (**14**) figures one in *Juglans nigra*. Within a period of six to eight days the megasporocytes of *C. glabra* pass through all the phases of synizesis and both of

[2] Figs. 5–12 constitute pl. I.

FIGS. 1–4.—Fig. 1, carpellate inflorescence of *J. mandshurica* 2 days after pollination. Fig. 2, same May 23, about 10 days after pollination. Fig. 3, same June 25, branch bearing nearly mature fruits. Fig. 4, same of *C. glabra*, May 25, about 10 days after pollination period.

the meiotic divisions, and have reached the megaspore stage or one of the early stages in gametophyte development at the time of pollination (figs. 25, 26). Heterotypic prophase ordinarily extends through a period of five to six days. In all material of *Carya* examined, the mother cell develops a linear tetrad of megaspores (fig. 25), the chalazal megaspore functioning as the embryo sac.

The individual ovulate flowers of *C. glabra* at pollination measure 10–12 mm. in length and 3–3.5 mm. in breadth. They are yellowish green and conspicuously glandular pubescent. The cupule (considered here as the specialized stem or enlarged receptacle) is marked in its upper section by four ridges, giving it a four-sided appearance and dividing it into four sections the margins of which are continuous with the edges of the sepals.

Longitudinal ridges or folds of the carpellary walls extend into the ovarian cavity, two of which, oriented in the plane of the carpels, grow conjointly with lateral extensions from either side of the axial placenta to form the median septum of the ovary. The problem of the septal vascular system and its relation to other bundles in the carpellate flower will be dealt with critically in a future paper. During early fruit development, all space within the ovary not occupied by the middle or primary septum and the enlarging ovule is filled with the light parenchymatous tissue of the endocarp, which takes its origin from the inner tissue of the carpel walls and from the septum. The origin of the endocarp, so-called "packing-tissue," is shown in figures 15–17. As fruit development progresses, two wedge-shaped sections of a second septum may be differentiated from the tissue of the endocarp on either side of and at right angles to the plane of the middle septum. Figure 8, a median longisection of the young fruit cut transverse to the plane of the septum, shows the expanse of parenchymatous tissue surrounding the enlarging ovule, also the initiation of the lignified tissue of the second septum at two points, one proceeding from the margins of the original septum and the other from the inner edge of the carpel walls. The two partitions, the median or original septum and the later formed second septum, divide the basal section of the ovary into four chambers which later are filled by the lobes of the expanding embryo sac and each with the half of a cotyledon.

POLLINATION.—Conflicting accounts have appeared concerning courses taken by the pollen tubes in different species of Juglandaceae. NAWASCHIN (12) found in *Juglans regia* that the pollen tubes do not pass down the stylar canal or traverse the ovarian cavity, but advance through the tissue of the style and of the ovary wall until opposite the insertion of the single ovule. They then leave the ovary wall and pierce the chalaza, branching freely in the nucellus. Male nuclei discharged into the embryo sac were seen "wandering" in its cytoplasm and fusing with one of several "free cells" that function as eggs but have not organized an egg apparatus. BILLINGS' observations (4) in *Carya olivaeformis* and NAWASCHIN'S (14) in *Juglans nigra* and *J. regia* are in essential respects in agreement with the preceding statement, except that NAWASCHIN in his later work describes and illustrates a rather well organized embryo sac with egg apparatus.

WOODROOF (22) also traces the pollen tubes of *Hicoria pecan* through the tissues of the style and ovary walls and observes that they approach the ovule opposite the plane of the middle septum, but she finds it necessary for the tubes to cross the narrow crevices which extend downward nearly to the base of the flower on either side of and parallel with the plane of the septum, and fixes the place of entrance of the tubes into the ovarian cavity as near the micropyle or at a point nearly opposite the chalaza. She finds that pollen tubes may enter the cavity of the ovary 6–12 hours after pollination, but do not enter the nucellus until the embryo sac is mature, about a week later, in the meantime growing about in the cavity and crevices.

In all the preparations of *Carya glabra* examined the nucellus is two-thirds to three-fourths inclosed by the integument at the time of pollination. Within two or three days after pollination the integument has closed firmly about the nucellus, with but a narrow crevice intervening. The pollen tubes advance through the tissue of the style, following the course of the inner set of vascular bundles to a point just above the ovarian cavity. Here they leave the vascular tissues, and, growing through the portion of the ovary wall later to be transformed into shell, pass directly to the apex of the ovarian cavity. This may require four to five days. The tip of the massive

integument is at this time in contact with the ovary wall; in fact the tissues of the two seem almost to fuse. Pollen tubes apparently invade the tissues of the integument at this point, and passing down through the integument to the base of the nucellus, approach the embryo sac from the chalaza. The interval between pollination and fertilization is slightly over two weeks, from 16 to 18 days. Pollen tubes enter the embryo sac by June 2 or 3, and always at the micropylar end of the sac.

Cases have been found in which pollination without subsequent fertilization seemed sufficient to start fruit development; in fact, fruits may reach a size of 15×7.5 mm. and contain an ovule in which an embryo sac has never appeared.

FERTILIZATION.—Fusion of the polar nuclei precedes entrance of the pollen tube into the embryo sac (fig. 27). The primary endosperm nucleus, the dominating figure of the mature embryo sac, is usually located in the upper section of the sac (figs. 28, 29), and prior to enlargement of the sac is lodged just beneath the egg apparatus. A well defined membrane separates the egg nucleus from the synergids, with the synergid nuclei usually nearer the micropyle. Generally sections of the ovule and embryo sac made perpendicular to the plane of the middle septum show the saclike synergids overlying and partially concealing the egg (figs. 27, 28); occasionally sections cut in that plane show the orientation of the egg apparatus with both synergids appearing to one side of the egg (fig. 29). Union of the endosperm nucleus and first male nucleus is in advance of that of the egg and second male nucleus, but the interval between the two fusions is but a matter of hours, and not two to three weeks as reported by WOODROOF (**22**) in the pecan. The unfertilized egg invariably displays only one nucleolus; after fertilization there are two (figs. 30, 38). No internal change in the zygote is noted for a period of 17–18 days. The definitive nucleus divides immediately and endosperm accumulates rapidly in the upper section of the sac. In embryo sac material fixed June 3, 1931, two to three stages were observed: in one case a pollen tube was found taking a direct course past the egg to the endosperm nucleus with one male nucleus in contact with the primary endosperm nucleus; in other embryo sacs (slightly more advanced) remnants of a pollen tube were seen be-

tween the zygote and surviving synergid, and several endosperm nuclei in the vicinity of the zygote (fig. 30). It is not unusual in *Carya* to find at least one of the synergids surviving the passage of the pollen tube in the sac; in one case both were seen, one apparently fertilized, with the pollen tube closely applied to one side of the egg.

Through the ensuing two weeks (June 1–15) the embryo sac gradually advances on the surrounding nucellar tissue, and the endosperm is seen to form a thin but complete lining for the sac (fig. 17). Passing through the stage of free nuclei, it eventually forms cell partitions, first at the apex and base of the sac and later throughout. There may be enlargement of the embryo sac and of the entire ovule, and some development of endosperm even though a proembryo fails to appear in the sac. But expansion ceases after a period of 12–14 days, in the absence of a fertilized egg or a young proembryo, and a noticeable "drop" of fruit is found to occur at this time, about 50 per cent of the season's loss between June 12 and 15. Two similar embryos may appear in the embryo sac of *Carya glabra*, one in the position of the egg and the other in that of a synergid; only one ever passes beyond the proembryonic condition.

In regard to the synergids, NAWASCHIN and FINN (**14**) observed in *Juglans* that prior to fertilization not only one but both synergids become cloudy and disintegrate. So far as the fertilized egg is concerned, this remains for some time in an apparently unchanged state before its first division, often with many endosperm nuclei in the embryo sac.

EMBRYO.—The first division of the fertilized egg occurs about June 20, nearly three weeks after fertilization and five weeks after pollination. WOODROOF (**22**) reports the first division of the egg of the pecan eight to nine weeks after pollination, SHUHART (**16**) three to four weeks.

In the plasma-rich end of the elongating egg (fig. 38) two cells are separated by a wall which may be horizontal or slightly oblique. Of the two sections thus formed, the smaller apical one (*A*) contributes to the formation of the cotyledons and stem tip of the embryo, while the meristem of the root axis and the suspensor are derived from the basal section (*B*). Deviating from the procedure generally characterizing the proembryo of dicotyledons, the apex section does not

form quadrants, but is divided into three sections (fig. 39) by two vertical walls: the first one diagonal, dividing the apex cell into two wedge-shaped portions; the second also diagonal, dividing equally the larger of the two sections formed from *A*.[3] A third division, vertical and at right angles to the plane of the first two partitions, creates from the three sectors an apical group of six cells. From the lateral sections of this group, through subsequent sectioning, the two deeply bilobed cotyledons develop; from the central section comes the meristem out of which the vegetative point of the stem proceeds. This central section bears some resemblance to the "epiphyse" of the proembryo of *Geum* and *Myosotis* (**17, 18**), also to the wedge-shaped apical cells appearing occasionally in the proembryonic development of *Salix* (**5**).

While segmentation in the apical cell is in progress, the larger basal cell has undergone division, usually horizontal. Partitioning in the middle cell so formed is variable; nevertheless to this region can be traced the hypocotyl and the initial zone of the root tip. The basal cell formed from *B* develops the first formed portion of the root cap and the short, multicellular suspensor.

By July 11 the embryo is seen as a small spherical mass of cells inclosed by a delicately constructed cellular endosperm (figs. 42, 43). For a period of 8–10 days the embryo slowly enlarges, and by the third week in July has become a pear-shaped body (figs. 44, 45), the apical two-thirds of which is characterized by considerable meristematic activity, cell division occurring less frequently in that section of the embryo directed toward the micropyle. In the developmental stages immediately following, two meristematic areas become especially prominent: an apical one (characterized by the predominance of longitudinal divisions) from which the initials of the epicotyledonary axis take their origin, and a wedge of initials in the median third of the proembryo from which the primary meristems of the root tip are derived. For a time the periblem and plerome of the root axis develop from a common meristem, and are scarcely distinguishable as distinct regions. In the course of later embryo development, however, with the appearance of the narrow, elongated

[3] The first two vertical divisions are generally transverse to the plane of the carpels and the median septum of the ovary.

provascular elements, the periblem and plerome are distinctly recognizable, and long before the completion of intraseminal development become clearly differentiated right to the initials of the root apex (fig. 49). The dermatogen of the root, and a root cap-renewing initial layer are differentiated from the border of the apical meristem of the root tip.

As in *Ginkgo* (**11**), the primordia of the two cotyledons arise as crescentic mounds of tissue in the marginal region of the apical meristem of the proembryo (fig. 46), commencing their development almost simultaneously with organization of the meristems of root and stem tip. For a time their development precedes that of the stem meristem. By the latter part of July they are differentiated as winglike structures which develop slowly, first at right angles to and later in the plane of the middle septum, the septum eventually forming a deep partition separating the halves of the cotyledons and not the two cotyledons, as reported by WOODROOF (**21**) and ADRIANCE (**1**). Figures 47 and 50 show clearly the orientation of the primary regions of the embryo body in respect to the micropylar axis, also with reference to the middle septum, for both are at right angles to the plane of the middle septum. Most of the detailed drawings of stages in embryo development both in *Carya* and in *Juglans* have been from sections made in the plane of the middle septum, since this afforded the better view of the developing cotyledons. The bilobed character of the cotyledons becomes apparent early in August (about six weeks after the first division of the egg), when the entire embryo is little more than 1 mm. in length (fig. 50). The six primary procambial units of each cotyledon are observed to unite in pairs at the cotyledonary node or just above it, and as double strands they meet and are inserted on the desmogen of the primary root.

A broad, slightly elevated epicotyledonary axis bearing in its center three successive horizontal groups of initials (fig. 51) is recognized, surrounded by the bases of the enlarging cotyledons the latter part of July or early in August. The primordia of the first foliar organs appear without delay, and, as at the terminal apices of *Carya* seedlings (**10**), succeeding primordia follow one another so closely that it soon becomes difficult to distinguish the vegetative point and its initials. A plumular bud consisting of 6–8 young scale

leaves and the primordium of the first foliage leaf is organized late in August.

II. JUGLANS MANDSHURICA

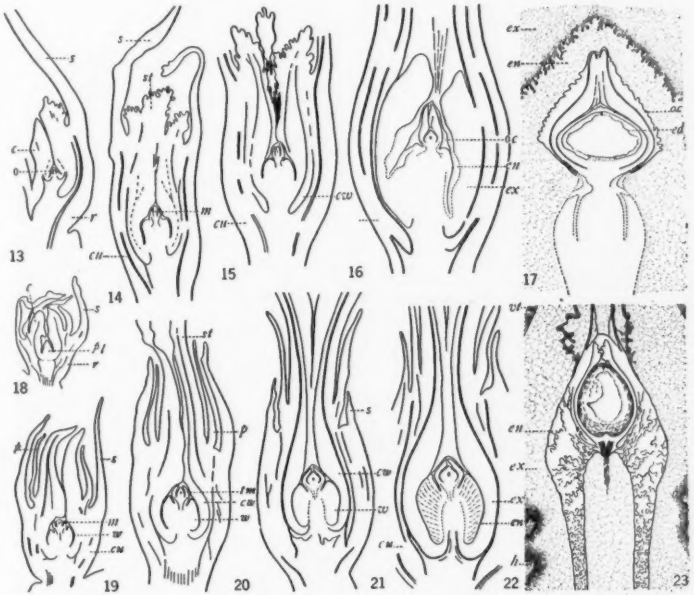
CARPELLATE FLOWERS.—Female flowers, eight to ten on a short spike terminating the shoot of the season, become visible above the leaves of the shoot early in May. Contrasting with the situation in *Carya glabra* is that found in *J. mandshurica*, in which practically all of the flowers in each ovulate head reach full development and are receptive at pollination time (fig. 1). Furthermore, a high percentage of the flowers are pollinated and continue in fruit development (figs. 2, 3).

The individual flowers are olive green, globose to ovate in form, and prior to and during the pollination period are clothed with reddish sticky hairs. Each bears two prominent brick red, plumelike stigmas which give to the carpellate inflorescence a peculiarly ornate character.

The ovulate flower is composed of two carpels inclosed by a fleshy cup-shaped receptacle or cupule, the foliar structures bordering the carpels and borne at the summit of the receptacle constituting the inner and outer members of a perianth. The order of succession of floral cycles is here interpreted as: outer members of perianth, carpels and inner members of perianth, and stamens (when present). Small abortive stamens have been observed to occur occasionally in early stages of development of the carpellate flowers of *Juglans mandshurica*. The inner set of members of the perianth do not appear in the carpellate flowers of *Carya*, nor do the stamens.

The interpretation of cupule structure suggested here is not in agreement with the generally recognized definition of the cupule as "an involucre of bracts adherent by their base." BENSON (3) has described the fertile flowers of *Juglans* as "composed of two carpels inclosed by a four-toothed calyx, and a cupule of several bracts all united in such a manner that only their upper portions are free." A detailed study of a series of stages in floral development, both in *Carya* and *Juglans* (figs. 13–17 and 18–23), has led to the conclusion that the cupule, at least of the Juglandaceae, is not to be regarded as an involucre of bracts adherent by their base, but rather as a specialized stem or receptacle, and this conclusion appears also to have

been reached by SHUHART (**16**) in his study of the pecan. This point will be treated at greater length in a later paper.



FIGS. 13–23.—Figs. 13–17, *Carya glabra;* figs. 18–23, *J. mandshurica.* All are median vertical sections of ovulate flowers or young fruits, collected from May 5 to June 22: Fig. 13, early stage in development of one of basal flowers showing central placenta and young ovule, differentiating carpels and enlarged outer sepal. Figs. 14, 15, floral development shortly before pollination. Fig. 16, development of flower and ovule at time of fertilization. Fig. 17, ovule about 3 weeks after fertilization. Endosperm within enlarging embryo sac is in free nuclear condition; 3-celled embryo at apex of sac. Figs. 18–20, young ovulate flowers of *J. mandshurica.* Fig. 21, flower and ovule at pollination. Fig. 22, same at fertilization. Fig. 23, about 2 weeks after fertilization showing ovule with embryo sac with parietal layer of endosperm, also 18–20-celled embryo at apex of sac. Endocarp in a partially disorganized condition. All sections cut 10–12 μ and most of them transverse to plane of septum (*c*, carpel; *cw*, carpel wall; *cu*, cupule; *en*, endocarp; *ex*, exocarp; *ed*, endosperm; *h*, husk; *m*, megasporocyte; *oc*, ovarian cavity; *pl*, placenta; *r*, receptacle; *s*, sepal; *st*, stigma; *w*, winglike evaginations of placenta).

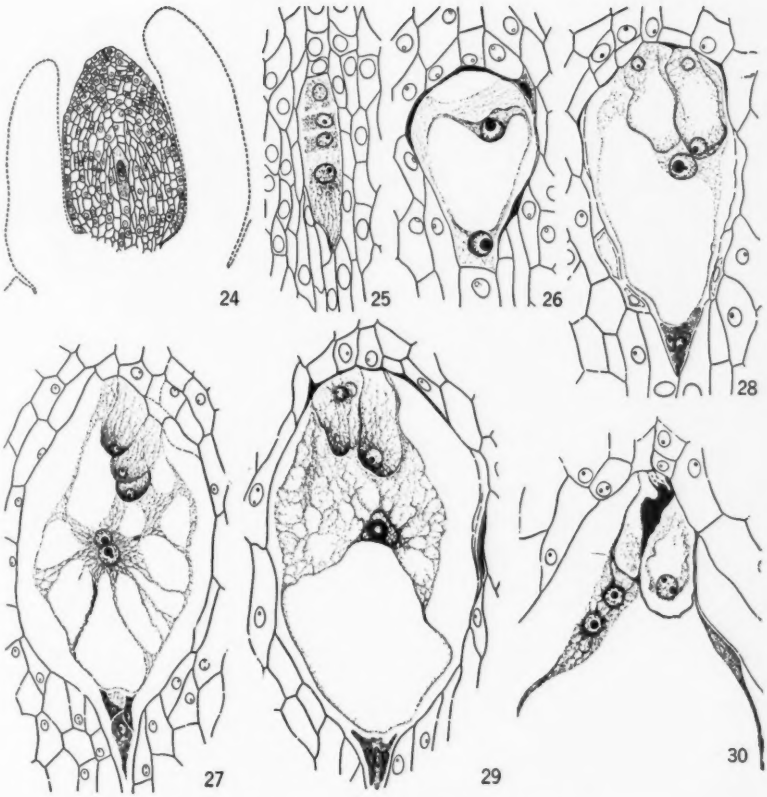
A vertical partition, located in the plane of the stigmas and carpels, supports the single orthotropous ovule and divides the basal part of the ovary into two chambers. As in *Carya*, most of the space

within the ovary not occupied by this partition and the ovule (fig. 9) is filled with the soft white tissue of the endocarp. Unlike that of *Carya*, the endocarp in *Juglans* takes its origin as winglike outgrowths from the placenta, developing at right angles to the plane of the septum. This is well illustrated in figures 18–22, also figure 9. Shortly before pollination, and for an interval of five or six days following, the endocarp exists in a rather compact state, completely filling the ovarian cavity and crowding close about the base of the ovule (figs. 21, 22); but with growth of the ovule and later expansion of the seed coat it is forced from the vicinity of the ovule, gradually becoming broken and chaffy in character (figs. 10, 23).

One of the unique features of ovule development in *J. mandshurica*, and of somewhat frequent occurrence here, is the appearance of a double nucellus in a single ovule, a sort of bisporangiate condition, in which a single massive integument incloses both megasporangia. This condition will be found at early stages of ovule development, at the mother cell or megaspore stage, never later. The manner of origin and the ultimate fate of one or both of the nucelli in such cases have not been determined.

Ordinarily the nucellus is more than three-fourths inclosed by the integument at the time of pollination (fig. 21), and by the time of fertilization (5–6 days later) the integument completely invests the nucellus (fig. 22), growing close to the apical wall of the ovarian cavity.

POLLINATION AND FERTILIZATION.—Pollination is first evident about May 6, and four to five days are generally required for the tubes to reach the embryo sac. As in *Carya*, the pollen tubes advance through the tissues of the style following rather closely the course of the vascular bundles. The direction of growth of the tubes after reaching the vicinity of the ovary is various. They may leave the vascular tissue at this point, and, growing through the upper part of the carpel wall, pass directly to the apex of the ovarian cavity; or they may continue to follow the general course of the vascular bundles bordering the carpel wall, at intervals branching out and invading the tissue of the wall. Whatever their course in the wall of the ovary, those reaching the vicinity of the embryo sac proceed around



FIGS. 24–30.—*Carya glabra:* Fig. 24, ovule shortly before pollination, megasporocyte in pachytene; ×149. Fig. 25, linear tetrad of megaspores; ×250. Fig. 26, 2-nucleate embryo sac; ×250. Fig. 27, embryo sac at union of polar nuclei. Definitely organized egg apparatus at micropylar end of sac; ×149. Fig. 28, mature embryo sac. Primary endosperm nucleus lodged just beneath the egg, its characteristic position prior to entrance of pollen tube; ×250. Fig. 29, mature embryo sac. Both synergids distinguishable at left of egg, one partially concealed by the other; ×250. Fig. 30, embryo sac shortly after fertilization. Remnants of pollen tube between zygote and surviving synergid, also two of several endosperm nuclei in vicinity of zygote; ×250.

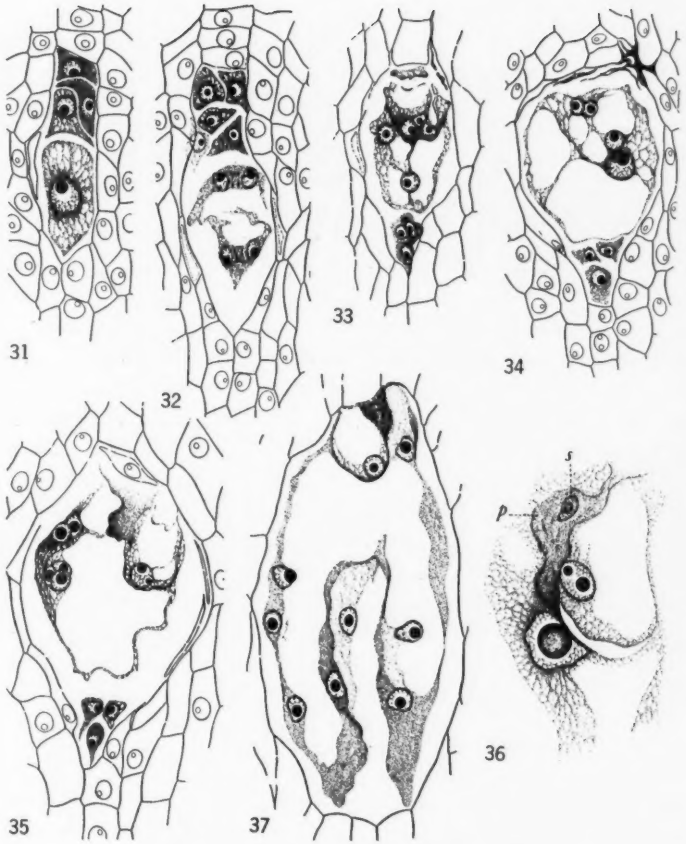
the base of the ovarian cavity and approach the ovule by way of the vascular tissues of the placenta.

The megasporocytes of *J. mandshurica* pass through the different phases of meiosis within three to four days, and embryo sacs are in one of the earlier stages of nuclear division at the time of pollination. Embryo sacs in the more advanced flowers collected May 7 of the past season were in one of the later stages of nuclear division, mostly 8-nucleate (fig. 33). In some the polar nuclei were seen in contact (fig. 34); in others, fusion of the polar nuclei had been effected. There is a noticeable shortening of the intervals here as compared with *C. glabra*, where 15–16 days were found to elapse between the megaspore stage and the mature embryo sac.

More than one pollen tube was not observed to enter the embryo sac of *C. glabra*, but in *J. mandshurica* it is not unusual to find evidence of two tubes, both entering from the micropylar end. The more common route is to one side of and in contact with the egg, usually passing between the egg and the synergids (fig. 36). One or possibly both of the synergids may be destroyed by the passage of the tube or tubes in the sac, but both are in evidence prior to their entrance, and frequently one persists after fertilization (fig. 36). This was found also to be the case in *Carya*. NAWASCHIN and FINN (**14**) observed several "content-conducting" tubes on their way to the egg apparatus. Sometimes the contents of one pollen tube had already emptied and located in the vicinity of the egg apparatus; at other times the contents of several pollen tubes were found around the already fertilized egg, forming a uniform mass which contained several "sperm-cell-pairs." They also reported disintegration of both synergids prior to fertilization.

In *J. mandshurica*, fertilization of the egg and the primary endosperm nucleus are not simultaneous. The male nuclei reach both at about the same time, but an interval of several hours may intervene between the two fusions. As in *Carya*, the definitive nucleus divides immediately, often before union of the egg and sperm nucleus is complete (fig. 35).

EMBRYO.—Again contrasting with the situation observed in *C. glabra*, in *J. mandshurica* only six to seven days intervene between the first division of the definitive nucleus and that of the zygote. In young



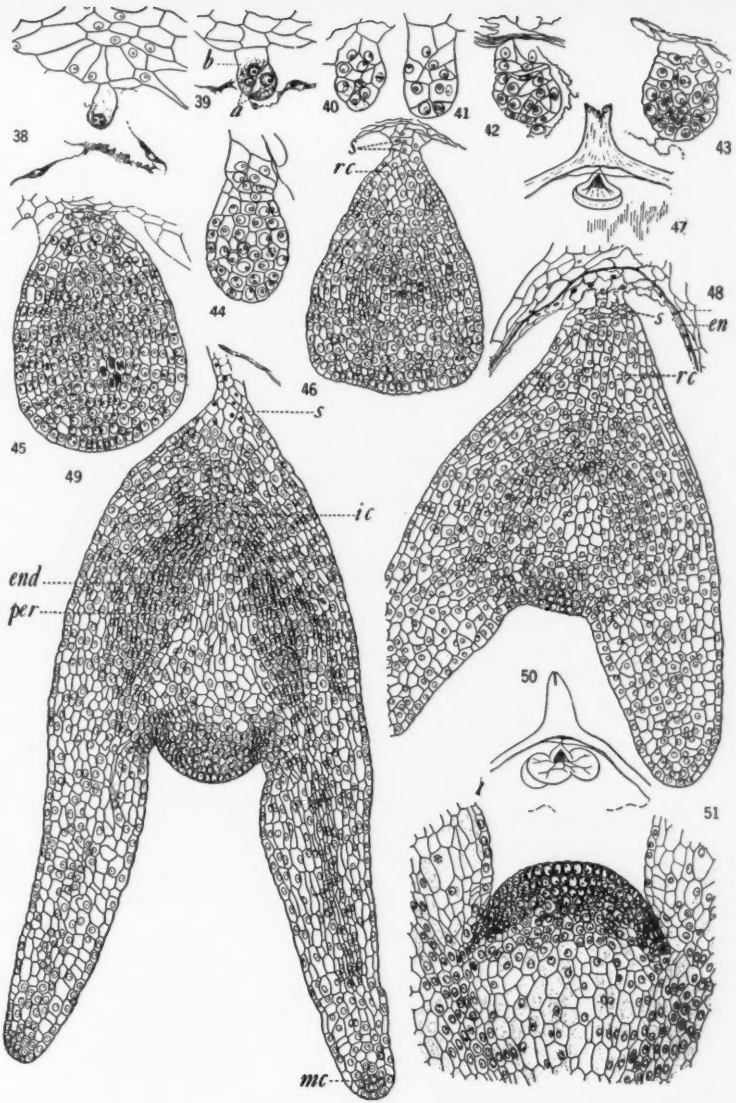
FIGS. 31–37.—*Juglans mandshurica:* Fig. 31, tetrad of megaspores, megagametophyte obviously developing from basal one; ×334. Fig. 32, 4-nucleate embryo sac; ×334. Fig. 33, 8-nucleate embryo sac in early stage of organization of egg apparatus. Antipodals and polar nuclei distinguishable; ×334. Fig. 34, embryo sac prior to union of polar nuclei (lodged at right of egg, one partially concealed by other); ×334. Fig. 35, embryo sac after entrance of pollen tube, seen applied to one side of zygote. First endosperm nuclei lodged in upper left corner of sac; ×400. Fig. 36, embryo sac directly after fusion of egg and sperm nucleus and before first division of definitive nucleus; ×500. Fig. 37, embryo sac several days after fertilization with abundant endosperm but zygote as yet undivided; ×334.

fruits collected May 18 the zygote was as yet undivided, but the endosperm was found to be in an advanced state of free nuclear division, each nucleus with two to several large nucleoli (fig. 52). A 4–8-celled embryo appears in fruits collected May 23, and by May 27 an enlarged embryo sac with a well defined parietal layer of endosperm occupies most of the nucellus (figs. 10, 23). Development and differentiation of the endosperm and embryo proceed rapidly from this point, and by June 15 (4–5 weeks after pollination) the seed coat has expanded about to full size, extending into nearly all available space within the shell, by its growth greatly enlarging the ovarian cavity. Endosperm, cellular throughout, fills the greater part of the apical section of the embryo sac, and as a layer of varying thickness lines each lobe of the sac (figs. 11, 12).

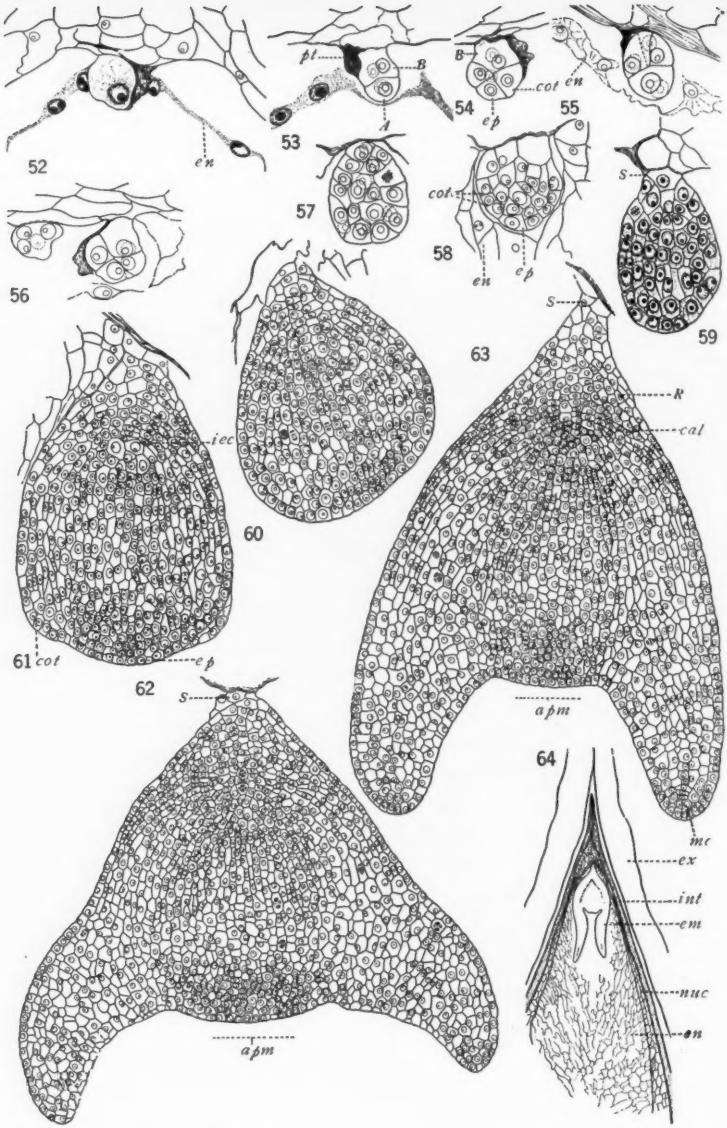
Segmentation in the proembryo of *J. mandshurica* is essentially the same as in *C. glabra*, except that greater irregularity occurs. The first division of the egg is horizontal, forming two nearly equal sections, *A* and *B*. From the apical cell (*A*) through later sectioning the cotyledons and stem tip are derived; from the basal cell the hypocotyledonary region and the suspensor. Ordinarily the apical cell is divided, as described in *Carya*, by two obliquely opposed walls (figs. 54, 56). A third division, vertical but at right angles to the plane of the first two, forms from the three sectors an apical group of six cells.[4] From the lateral sections of this group the two winglike cotyledons develop, and from the central section comes the meristem from which the initials of the stem proceed. Partitioning in the basal cell (*B*) is extremely variable; nevertheless in some of the clearer preparations it is possible to distinguish a primary horizontal wall in *B*. From the middle section so formed the initial zone of the root tip apparently develops; from the basal cell formed by *B* a section of the root cap and an abbreviated suspensor.[5] In the course of de-

[4] The first longitudinal division of the apex cell may be in the plane of instead of transverse to the plane of the carpels, as is the more common procedure. Furthermore, exceptions occur in which quadrant cells arise out of *A*, and obliquely placed walls in the apical quadrants separate the cotyledonary part of the embryo from the "epiphyse." The latter course also appears in *Juglans nigra*.

[5] Differentiation of the proembryo body into two primary regions (rather than three) corresponding to the apical and basal cells formed at the first horizontal division of the zygote is found to occur occasionally in *J. mandshurica* and is also seen in *J. nigra*. In



FIGS. 38–51.—*Carya glabra:* Fig. 38, zygote shortly before division. Figs. 39–46, 48, 49, stages in segmentation of proembryo and development of embryo. Figs. 47, 50, dissections of apical portions of enlarged embryo sacs, showing orientation of embryos with reference to middle septum, also micropylar axis (both at right angles to plane of septum). Fig. 51, epicotyledonary axis bearing in its center three successive horizontal groups of initials (*A*, apical section of proembryo; *B*, basal section of proembryo; *apm*, meristem of stem tip; *ic*, initials of periblem and plerome of root tip; *mc*, apical meristem of cotyledon; *en*, endosperm; *end*, endodermis; *per*, pericycle; *rc*, root cap; *s*, suspensor). Figs. 38–46, ×125; figs. 48, 49, ×82.5; figs. 47, 50, ×3.5; fig. 51, ×250.



FIGS. 52–64.—*Juglans mandshurica*, stages in segmentation of proembryo and development of embryo. All embryos sectioned in plane of septum except fig. 62, which is transverse to that plane and shows detail of embryo seen at apex of embryo sac in fig. 12: *A*, apical section of proembryo; *B*, basal section of proembryo; *apm*, meristem of stem apex; *iec*, initials of periblem and plerome of root axis; *cal*, calyptrogen; *en*, endosperm; *cot*, cotyledonary sector; *ex*, exocarp; *in*, integument; *nuc*, nucellus; *mc*, apical meristem of cotyledons; *pt*, pollen tube; *r*, primary root; *s*, suspensor. Figs. 52–57, ×188; figs. 58, 59, ×150; figs. 60, 61, ×110; figs. 62, 63, ×82.5.

velopment of the embryo the suspensor cells became so compressed as to be almost unrecognizable.

Embryological development from this point is substantially the same as outlined in *Carya*, but proceeds more rapidly. Within a period of three to four weeks, the embryo passes through all the stages in the origin and early differentiation of the primary regions of the embryo body. Orientation of the cotyledons is the same as in *Carya*, that is, transverse to the plane of the middle septum of the fruit. Their bifurcated character is early apparent, and long before the embryo in its development reaches the tip of the septum. An apical meristem is a characteristic feature of the young cotyledons (figs. 62, 63), and is retained for a time, even after their bifurcation, as an embryonic region at the tip of each cotyledonary lobe.

ENDOSPERM.—In *J. mandshurica* this is more abundant than in *Carya*. A "free nuclear" period, of four to five days' duration, is characterized by the total absence of achromatic figures, suggesting an amitotic division of the nuclei at this time. The endosperm eventually forms a parietal plate of cells which gradually advances from the wall of the embryo sac, leaving a narrow sap-containing central region in each lobe of the sac. The cotyledons in their elongation extend between the marginal layers of the nucellus and the endosperm, in the course of their expansion gradually inclosing the inner mass of endosperm, resorbing its substance, and reducing it to a shapeless mass.

Summary

1. The ovulate flowers both of *Carya* and *Juglans* consist of two carpels inclosed by a fleshy, cup-shaped receptacle or cupule. The foliar structures bordering the carpels and borne at the summit of the receptacle are interpreted as a perianth. Small abortive stamens occur occasionally in early stages of development of the carpellate flowers of *J. mandshurica*. In the ovulate flowers of *Carya*, neither the inner set of members of the perianth nor the stamens develop.

2. In the carpellate flowers of the Juglandaceae, an internal vertical partition (in *Juglans* and *Carya* oriented in the plane of the car-

such cases the apex section has been observed to contribute the meristem of cotyledons, epicotyledonary axis, and even that of the root axis; the less active basal section produces the suspensor and a section of the root cap.

pels) supports the single large, sessile ovule. As fruit development progresses in *Carya*, two wedge-shaped sections of a second septum are differentiated from the tissue of the endocarp, on either side of and at right angles to the middle septum. This second septum does not appear during the development of the young fruit of *J. mandshurica*.

3. The megasporocyte is distinguishable in the young ovules, both of *C. glabra* and *J. mandshurica*, as a slightly enlarged cell lying deep in an axial strand of the nucellus, the phases of meiosis occupying six to eight days in *C. glabra;* in *J. mandshurica*, three to four days. A linear tetrad of megaspores is formed in both, the megagametophyte developing from one of the two inner megaspores.

4. In *C. glabra*, 15–16 days elapsed between the early megaspore stage and the mature embryo sac; in *J. mandshurica*, five to six days.

5. The megagametophytes of *C. glabra* and *J. mandshurica* are normal angiosperm types in their development, and alike in essential features. That of *C. glabra* is larger than the gametophyte of *J. mandshurica* and presents a more definitely organized egg apparatus. One, in some cases both, of the synergids are destroyed by the passage of the pollen tube or tubes in the sac; but both are in evidence prior to entrance of the tubes, and frequently one persists after fertilization. In *Carya* the surviving synergid may produce a small proembryo.

6. There is an interval of 17–18 days between fertilization and the first division of the zygote in *C. glabra;* in *J. mandshurica*, six to seven days. In both the definitive nucleus divides immediately, a parietal layer of endosperm being one of the distinctive features of the enlarged embryo sac prior to division of the zygote.

7. Deviating from the procedure generally characterizing the proembryo of dicotyledons, the apex cell of the young proembryo in *Carya* and *J. mandshurica* does not form quadrants, but is divided by two obliquely opposed walls into three sectors. A division, vertical and at right angles to the plane of the first two partitions, creates an apical group of six cells. In general the plane of the two cotyledons and that of the long axis of the stem tip coincides with the position of the three primary sectors of the apical section of the proembryo.

8. Segmentation in the basal section of the globular proembryo is variable, especially in *Juglans;* nevertheless to this section may ordinarily be traced the initials of the root axis, the root cap, and an abbreviated multicellular suspensor.

9. In its flower, ovule, gametophyte, and embryo features, *Juglans* may be said to present characters of greater phylogenetic interest than does *Carya*. On the other hand, the larger and more definite character of the embryo of *Carya*, both in proembryonic and embryonic phases, makes this more valuable for a histogenetic study.

The writer wishes to acknowledge her indebtedness to Dr. D. S. JOHNSON, through whose courtesy extensive collections of material were secured from the Botanical Gardens and Arboretum at Johns Hopkins University, to Dr. E. A. ANDREWS of Johns Hopkins University for a series of collections of *Juglans mandshurica*, and to Dr. C. J. CHAMBERLAIN of the University of Chicago for helpful criticism during the progress of the study.

Grateful acknowledgment is also made for two generous grants received from the National Research Council, in aid of a comparative study of the embryogeny of the Juglandaceae and Fagaceae. Valuable technical assistance has been rendered by Mr. B. L. HAMMOND.

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LITERATURE CITED

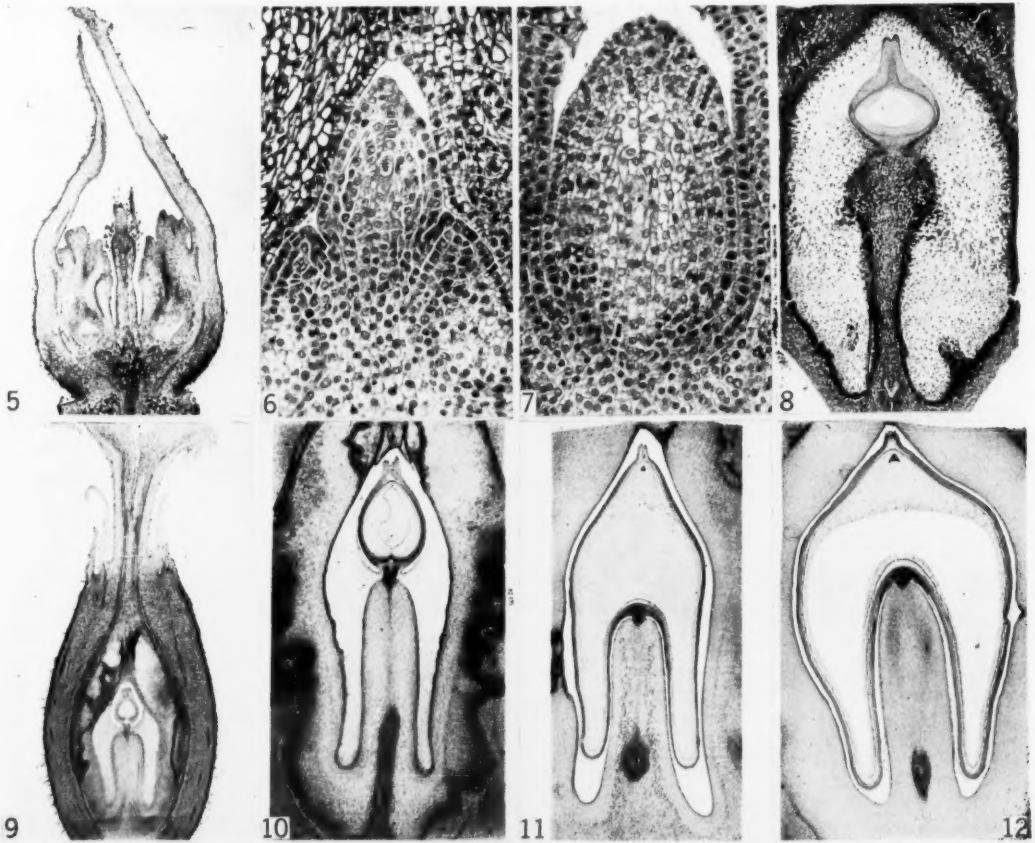
1. ADRIANCE, G. W., Factors influencing fruit setting in the pecan. BOT. GAZ. 91:144–165. 1931.
2. BENSON, MARGARET, Contributions to the embryology of the Amentiferae. Part I. Trans. Linn. Soc. Bot. II. 3:409–424. 1894.
3. BENSON, MARGARET, and WELSFORD, E. J., The morphology of the ovule and female flower of *Juglans regia* and of a few allied genera. Ann. Botany 23:625–633. 1909.
4. BILLINGS, F. H., Chalazogamy in *Carya olivaeformis*. BOT. GAZ. 35:134–135. 1903.
5. CHAMBERLAIN, C. J., Contribution to the life history of *Salix*. BOT. GAZ. 23:147–178. 1897.
6. DE CANDOLLE, C., Mémoire sur la famille des Juglandées. Ann. Sci. Nat. Bot. Ser. IV. 18:5–48. 1862.

7. CONRAD, A. H., A contribution to the life history of *Quercus*. BOT. GAZ. **29**: 408–418. 1900.
8. KARSTEN, G., Über die Entwickelung der weiblichen Blüthen bei einigen Juglandaceen. Flora **90**:316–333. 1902.
9. LANGDON, LADEMA M., Sectioning hard woody tissues. BOT. GAZ. **70**:182–184. 1920.
10. ———, Development and vascular organization of the foliar organs of *Carya cordiformis*. BOT. GAZ. **91**:277–292. 1931.
11. LYON, H. L., The embryogeny of *Ginkgo*. Minn. Bot. Studies **3**:275–290. 1904.
12. NAWASCHIN, S., Ein neues beispiel der Chalazogamie. Bot. Centralbl. **63**: 353–357. 1895.
13. ———, Über die Befruchtung bei *Juglans regia* und *J. nigra*. Trav. Soc. Imp. Nat. St. Petersbourg **28**:1897.
14. NAWASCHIN, S., and FINN, U., Zur Entwickelungsgeschichte der Chalazogamen. *Juglans regia* und *J. nigra*. Mem. Acad. Imp. Sci. St. Petersbourg **31**:no. 9. 1–59. 1913.
15. NICOLOFF, M. TH., Sur le type floral et le développement du fruit des Juglandées. Jour. Bot. Paris **18**:134–152; 380–385. 1904. **19**:63–68; 69–84. 1905.
16. SHUHART, D. V., Morphology and anatomy of the fruit of *Hicoria pecan*. BOT. GAZ. **93**:1–20. 1932.
17. SOUÈGES, RENÉ, Développement de l'embryon chez le *Myosotis hispida*. Bull. Soc. Bot. France **70**:385–401. 1923.
18. ———, Développement de l'embryon chez le *Geum urbanum* L. Bull. Soc. Bot. France **70**:645–660. 1923.
19. STUCKEY, H. P., The two groups of varieties of the *Hicoria pecan* and their relation to self-sterility. Georgia Agric. Exp. Sta. Bull. 124. 127–146. 1916.
20. WOODROOF, J. G., and WOODROOF, NAOMI, Fruit-bud differentiation and subsequent development of the flowers of *Hicoria pecan*. Jour. Agric. Res. **33**:677–685. 1926.
21. ———, Development of the pecan nut (*Hicoria pecan*) from flower to maturity. Jour. Agric. Res. **34**:1049–1063. 1927.
22. WOODROOF, NAOMI, Development of the embryo sac and young embryo of *Hicoria pecan*. Amer. Jour. Bot. **15**:416–420. 1928.
23. ZIRKLE, CONWAY, The use of N-butyl alcohol in dehydrating woody tissue for paraffin embedding. Science. January 24, 1930.

EXPLANATION OF PLATE I

FIGS. 5–12.—Figs. 5–8, *Carya glabra;* figs. 9–12, *J. mandshurica*.

FIG. 5. Two partially matured basal flowers of ovulate inflorescence showing greatly enlarged outer sepal. Young ovule in flower located to right is at early archesporial stage. ×11.8.



LANGDON on EMBRYOGENY

FIG. 6. Ovule at archesporial stage (megasporocyte in synizesis). ×200.

FIG. 7. Ovule at later stage of development (megasporocyte in pachytene). ×200.

FIG. 8. Median longisection of young fruit transverse to plane of median septum, showing expanse of parenchymatous tissue surrounding enlarging ovule and early differentiation of secondary septum from tissue of endocarp. ×5.3.

FIG. 9. Median longisection of young fruit perpendicular to plane of septum, 3 days after pollination; carpellary walls and endocarp clearly defined, also vascular tissue extending between cupule and ovary wall. ×5.

FIG. 10. Median section of young fruit perpendicular to septum, about 2 weeks after fertilization. Ovule shows embryo sac with parietal layer of endosperm, also 18–20-celled embryo. Note irregular outline of carpel wall at border of receptacle. ×7.

FIG. 11. Median longitudinal view of nut showing embryo, endosperm, and developing testa. Embryo shows as small heart-shaped body at apex of sac. ×3.3.

FIG. 12. Longitudinal view of nut perpendicular to septum, 5 weeks after pollination. Seed coat has expanded to about full size, extending to all available space within the shell. A well defined layer of endosperm, cellular throughout, lines the seed coat, and an embryo with diminutive cotyledons is distinguishable at apex of sac. ×4.

INFLUENCE OF TEMPERATURE AND NUTRITION ON THE GROWTH AND DURATION OF LIFE OF CUCUMIS MELO SEEDLINGS[1]

THOMAS I. EDWARDS, RAYMOND PEARL AND SOPHIA A. GOULD

(WITH FIVE FIGURES)

Introduction

This paper is a report of experiments on the growth of *Cucumis melo* seedlings in darkness at five constant temperatures under aseptic conditions on agar made up either in distilled water or in Knop's solution, planned and carried out in a continuation of the seedling research program of this laboratory. Knop's mineral salt nutrient solution has been in general use for more than 60 years to supply the salt requirements of a multitude of plant species, and there was every reason to believe that in this instance, as in the others, it would induce greater growth than distilled water, as in fact it did. The specific questions which the present paper attempts to answer are these:

1. What is the relative degree of improvement in growth of seedlings of *Cucumis melo* at different temperatures with added mineral nutrients?

2. What effects do these added mineral nutrients have on the duration of life of the seedlings?

In previous publications from this laboratory, the influence of temperature on the growth and duration of life of *Celosia cristata* seedlings and on the growth of *Cucumis melo* seedlings grown under essentially the same conditions has been discussed by EDWARDS, PEARL, and GOULD (1) and by PEARL, EDWARDS, and MINER (4). The first paper (1) contains a review of the literature on the temperature relations of seedling growth.

[1] From the Department of Biology, School of Hygiene and Public Health, The Johns Hopkins University, Baltimore, Maryland.

Methods

The methods used in this experiment were the same as those previously described (**1, 4**) and found in other papers from this laboratory. They have been more fully discussed by PEARL (**3**) and only the essential features will be noted here. Seeds from a single melon were freed from their seed coats, weighed, and only those whose weights fell between 0.0195 and 0.0225 gm. were used. The seeds were immersed for one minute in 1:1000 $HgCl_2$ solution, rinsed once, and soaked for three hours in sterile distilled water in individual vials. They were planted in previously sterilized glass tubes 2 cm. in diameter and either 40 cm. long (for the 15° and 20° tests) or 44 cm. long (used at 25°, 30°, and 35° C.), containing 25 cc. of 1 per cent agar made up in Knop's solution in one series and in distilled water in another series. The tubes were closed with loosely fitting cotton stoppers. The seedlings were grown in darkness at the five constant temperatures just mentioned, and at 24-hour intervals from the time of the beginning of soaking the length of the hypocotyl was measured in red light.

Approximately 25 seeds were planted at each temperature. The grounds on which seeds or seedlings were removed from the experiment were: (1) failure to germinate; seven cases, four of them at 15°; (2) failure of primary root to enter the agar in the usual manner; three cases; (3) fungal contamination in two tubes; (4) abnormally slow hypocotyl growth of two seedlings; (5) so sharp a curvature of one hypocotyl that measurement became impossible. The only groups from which more than two seeds were discarded were the 15° ones.

Results and discussion

INFLUENCE OF TEMPERATURE ON SIZE

Certain influences of temperature and of the two kinds of nutrition on the development of *Cucumis* seedlings are illustrated in figure 1, which is arranged to combine the functions of illustration and graph and which shows the appearance of representative seedlings of each of the ten groups of seedlings at the time they reached their final size. At the time growth ceased in each group, a seedling whose hypocotyl had the same length as the mean of the group re-

ceiving the same treatment was selected to show typical root development, and was photographed at a standard distance from the

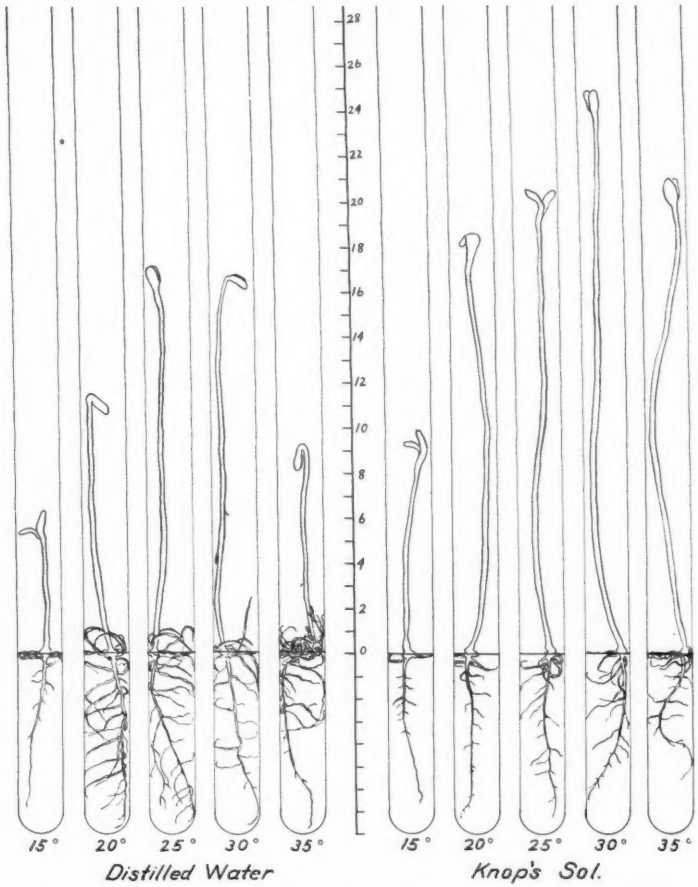


FIG. 1.—Representative *Cucumis melo* seedlings grown at five temperatures and with two kinds of nutrition at the time final size was attained. Scale reads in centimeters.

camera. Drawings were prepared from these photographs to the same scale.

In both series the greatest amount of hypocotyl growth occurred

at 30°, just as in another series of tests on seedlings of this species already reported (**4**), and the yields at the other temperatures fall along the usual type of optimal temperature curve. There are several conspicuous differences between growth on distilled water and growth on Knop's solution which figure 1 serves to illustrate. Considering each temperature separately, the hypocotyls grown on agar made up in the mineral salt solution are definitely taller than are those on plain agar. This difference is most pronounced at the temperature extremes, 15° and 35°, where the difference is almost 2:1, and it is least pronounced in the optimal temperature region at 25° and 30°. This is the same sort of relation as reported by TOMKINS (**6**) for the temperature relations of growth of several species of fungi in the presence or absence of nutrients, and which he expressed in the following words (p. 399): "At this stage in the enquiry a broad principle seems to emerge, namely, that when any one of the conditions is modified so as to favour growth, that is make it more rapid, the limitation of the growth rate by variation of any of the other conditions is rendered more difficult." "It would follow from this principle that any condition tending to retard growth . . . . would have least effect at the optimum temperature."

During the course of the measurements it became apparent that some groups of seedlings were more variable in height than others. The standard deviations and coefficients of variation of the final heights, together with their probable errors, are presented in a later section of this paper, and indicate which treatments resulted in relatively uniform seedlings and which were more variable in final height. To anticipate briefly these results here, it appears that in general the higher temperatures tend to have larger standard deviations than 15°; that is, there is a greater scatter of the individual seedling heights from the means. Such temperatures also produced taller seedlings, however, and the greater absolute heights create greater numerical differences among the seedlings. The coefficient of variation minimizes this discrepancy by reducing the measure of variation to a percentage basis, and comparison of the values for this constant shows that the greatest degree of uniformity was found in the optimal temperature range noted in the discussion of figure 1, 25° and 30° in the distilled water series, and 25°, 30°, and 35° in the

mineral nutrient solution series. These coefficients are somewhat low for biological material. The extremes of the temperature range in the distilled water series and the lower temperatures of the Knop's solution series produced the most variable seedlings. The coefficients of variation are high in the early stages of growth and fall rapidly at first.

The more vigorous hypocotyl growth on Knop's solution is accompanied by meager root growth, as compared with the distilled water series. The total amount of growth made by the roots does not show the same relation to temperature as hypocotyl development does; in fact, there seems to be an inverse relation between the two. In the distilled water series the heaviest root growth occurred at 20°, and this is confirmed by the dry weights. On account of the scanty root development on Knop's solution, the small differences in final size are not evident in the drawings. To judge from their dry weights, however, the greatest amount of root growth was found at 15°.

Often the junction of the root and the hypocotyl was raised above the level of the agar, and many secondary roots, especially in the distilled water series, did not enter the agar at all. Short adventitious roots appeared high up on numerous hypocotyls grown at 30° and 35° on distilled water agar, but they were not found under any other conditions of the experiments.

There is another kind of relationship (a minor one not clearly shown in figure 1 and one for which quantitative measurements are lacking) which fits into this scheme of internal regulations, namely, the degree of development of the petioles of the cotyledons. At high temperatures they are short; at low temperatures they are longer and appear to be extensions of the hypocotyl.

The means of the daily measurements of hypocotyl length are set forth in table I (A and B) and they appear in figure 2 as a pair of three-dimensional diagrams, one for the distilled water series and one for the Knop's solution series. These are constructed as though the growth curves for each of the five temperatures have been drawn on some material like cardboard, cut out, and set upright in proper order. At right angles runs another series of planes which may be regarded as indicating the relative heights of the hypocotyls 2, 4, 6

. . . . days after planting. The planes on which the growth curves are drawn are shown extended to the time of the beginning of death of the hypocotyls. To facilitate comparisons, numerals have been

TABLE IA

MEAN HEIGHTS IN CENTIMETERS OF CUCUMIS MELO HYPOCOTYLS FOR DIFFERENT INTERVALS AFTER PLANTING; DISTILLED WATER

DAYS	15°	20°	25°	30°	35°
2			0.22	1.14	0.81
3			1.15	3.44	1.80
4			2.98	5.72	3.15
5		0.33	5.12	8.23	4.25
6		0.91	7.13	10.95	5.47
7		1.65	9.59	12.92	6.64
8		2.88	11.43	14.36	7.22
9		4.39	12.93	14.97	7.79
10		6.04	14.15	15.57	8.19
11		7.21	14.89	15.94	8.46
12	0.17	8.32	15.26	16.20	8.72
13	0.30	8.94	15.47	16.39	8.85
14	0.40	9.46	15.58	16.44	8.88± .13
15	0.52	9.93	15.63± .09	16.45± .10	
16	0.64	10.36			
17	0.75	10.45			
18	0.95	10.67			
19	1.17	10.81			
20	1.39	10.86			
21	1.71	10.88± .11			
22	2.02				
23	2.33				
24	2.76				
25	3.21				
26	3.38				
27	3.68				
28	3.89				
29	4.09				
30	4.24				
32	4.36				
34	4.49				
36	4.61				
38	4.67				
40	4.70± .07				

placed on the graphs to indicate the actual final heights and durations of life of each group.

From these data it appears that in both series throughout the entire growing period the 30° hypocotyls were taller than those grown at any other temperature. In every instance the plotted points fall along S-shaped curves which rise a little more abruptly from the

base line in the distilled water series than in the Knop's solution series. This difference in form and the differences due to temperature will be discussed later in this paper. There is a tendency for growth to begin a little earlier on Knop's solution and to be terminated sooner than on plain agar. Considering each temperature

TABLE IB

MEAN HEIGHTS IN CENTIMETERS OF CUCUMIS MELO HYPOCOTYLS FOR DIFFERENT INTERVALS AFTER PLANTING; KNOP'S SOLUTION

DAYS	15°	20°	25°	30°	35°
2	.....	.....	0.34	1.59	0.78
3	.....	0.24	1.73	5.30	2.29
4	.....	0.81	4.67	9.84	4.74
5	.....	1.89	7.97	15.71	8.06
6	.....	3.79	11.91	19.85	11.96
7	.....	6.39	14.33	21.76	15.09
8	.....	9.46	16.02	22.62	17.14
9	.....	12.29	17.15	22.94	18.52
10	.....	14.49	17.92	23.03	19.04
11	.....	15.73	18.34	23.07	19.46
12	0.46	16.41	18.58	.....	19.66
13	0.63	16.74	18.68± .17	23.10± .20	.....
14	0.77	16.86	.....	.....	19.72± .16
15	0.91	16.97	.....	.....	.....
16	1.06	17.03	.....	.....	.....
17	1.37	17.07	.....	.....	.....
18	1.68	17.08± .17	.....	.....	.....
19	2.14	.....	.....	.....	.....
20	2.80	.....	.....	.....	.....
21	3.70	.....	.....	.....	.....
22	4.69	.....	.....	.....	.....
23	5.51	.....	.....	.....	.....
24	6.28	.....	.....	.....	.....
25	6.80	.....	.....	.....	.....
26	7.15	.....	.....	.....	.....
27	7.47	.....	.....	.....	.....
28	7.70	.....	.....	.....	.....
29	7.80	.....	.....	.....	.....
30	7.88	.....	.....	.....	.....
32	7.98	.....	.....	.....	.....
34	8.04± .11	.....	.....	.....	.....

separately, the distilled water series was longer lived than the better nourished series; and in each series duration of life was, with certain exceptions to be noted later, inversely proportional to temperature.

Unfortunately, during the tests on Knop's solution at 25°, the temperature control went out of order on the sixth day and the temperature fell to 23° for the rest of the growth period; this seems to

have reduced the final height somewhat in comparison with the performance at higher and lower temperatures.

Any attempt to compare the forms of the growth curves constructed directly from the data of table I is made difficult by the

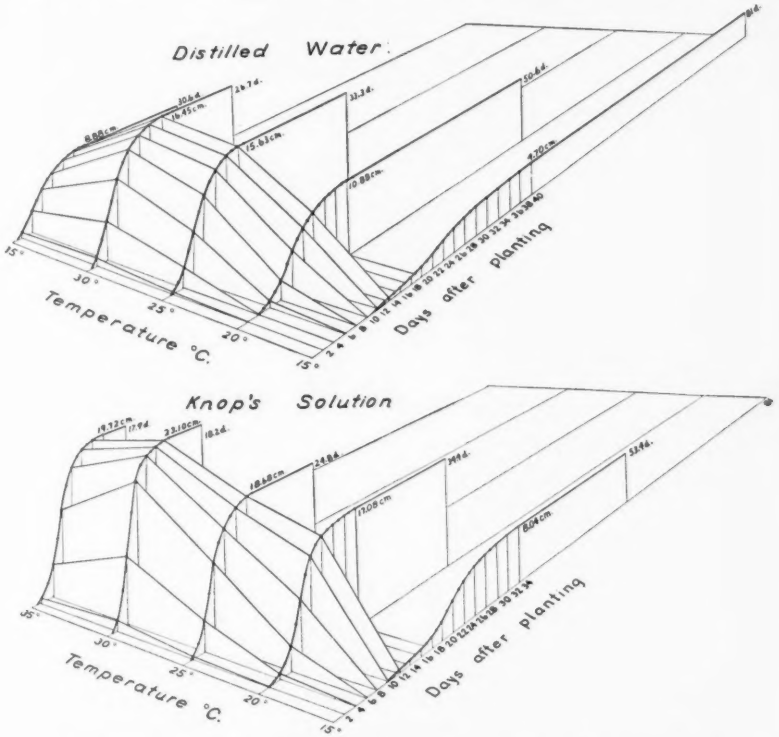


FIG. 2.—Three-dimensional diagrams showing course of growth and duration of life of *Cucumis* seedlings grown at five temperatures.

circumstance that the curves cover different time spans and in addition differ greatly in final size, as figures 1 and 2 illustrate. A simple arithmetical procedure introduced by PEARL, EDWARDS, and MINER (4) has been used to bring the ten curves into uniform scales of time and relative growth. The time from planting to the cessation of growth was taken as 100 per cent in each case, and the relative

heights for 10, 20, 30 . . . . per cent of the growing period were calculated by dividing the heights for these fractional growth periods by the final height, and multiplying by 100. Thus each curve starts at 0 on each scale and ends at 100. An example will illustrate this procedure. At 20° on Knop's solution, growth was considered to have ceased on the seventeenth day after planting. By interpolation, assuming that growth proceeded at a uniform rate between each pair of observations, the heights for 1.7, 3.4, 5.1 . . . . days were calculated (these periods constitute 10, 20, 30 . . . . per cent of the

TABLE II

APPROXIMATE RELATIVE YIELDS (MEAN HYPOCOTYL LENGTHS) AT STATED RELATIVE TIMES

GROWTH PERIOD (PER CENT)	PERCENTAGES OF OWN TOTAL YIELD									
	DISTILLED WATER SERIES					KNOP'S SOLUTION SERIES				
	15°	20°	25°	30°	35°	15°	20°	25°	30°	35°
10	.....	.....	1.0	5.2	6.4	.....	.....	1.2	3.8	2.8
20	.....	.....	7.4	20.9	18.1	.....	2.7	6.3	10.1	10.1
30	3.6	8.4	25.9	42.3	37.9	.....	12.2	23.4	28.9	27.4
40	13.6	26.5	45.6	66.6	56.1	8.8	34.4	46.9	52.8	52.7
50	29.6	55.6	67.2	82.8	74.8	17.0	63.7	70.2	77.1	76.5
60	58.7	76.6	82.7	91.0	83.9	39.3	86.3	83.9	91.0	89.7
70	82.8	87.1	92.9	95.6	91.3	76.2	95.7	92.2	96.9	96.2
80	92.8	95.4	97.6	98.4	95.8	93.5	98.5	97.4	99.2	98.9
90	98.1	98.3	99.3	99.7	99.1	98.4	99.6	99.1	99.8	99.8
100	100	100	100	100	100	100	100	100	100	100

growing period), these interpolated heights were divided by 17.07 (the height on the seventeenth day), and the quotients were multiplied by 100. These data are shown in table II and in graphical form in figure 3 as two families of sigmoid curves.

The distilled water curves have different degrees of symmetry; the low temperature curves do most of their growing relatively late in the growth period, the high temperature curves do most of their growing early. At 15°, for instance, less than one-third the final height was attained during the first half of the growth period, but at 30° more than four-fifths of the total growth had been accomplished in the same relative time. At 20°, 56 per cent of the total growth had

been completed at the midpoint of the growth period; at 25°, 67 per cent. At the only supra-optimal temperature tested, 35°, the value for the first tenth of the period is a little greater than the value for 30°, but thereafter growth was slower than at 30°.

The course of growth of seedlings supplied with mineral nutrients seems to have been much less affected by differences in temperature, to judge from the curves for the four higher temperatures in Knop's solution series. The curves for 30° and 35° take almost the

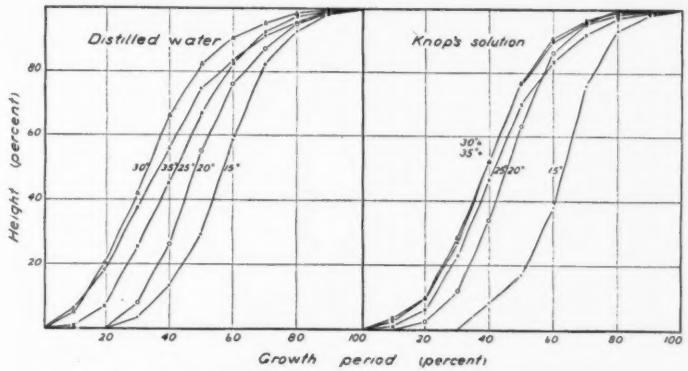


FIG. 3.—Growth curves showing percentages of final heights attained at expiration of various fractions of growth period.

same course, and those for 20° and 25° are not widely different. This is in agreement with the principle noted in the discussion of figure 1, that with improvement of the conditions affecting growth the influence of other modifying factors is lessened. Elongation began late in 15° and the growth curve is correspondingly delayed. The five curves of this series rise less steeply during the early periods than do the distilled water curves, but they compensate for this by relatively greater growth rates in the latter half of the growing period, a relationship which can be seen in figure 2 also.

DRY WEIGHTS

Several details of the experimental procedure need to be kept in mind in considering the dry weights presented in figure 4: (1) Seedlings were removed one by one as the hypocotyl of each showed the

first signs of death,—usually constriction of a zone near the cotyledons or the filling of the intercellular spaces of some part of the hypocotyl with water, giving it a translucent appearance. (2) Each seedling was cut up into cotyledons (including their petioles), hypocotyls, and roots, and the separate organs were dried at 98° and weighed. (3) The seedlings were grown under aseptic conditions throughout the entire experimental period and as a result they died from starvation rather than from bacterial or fungal attack. (4)

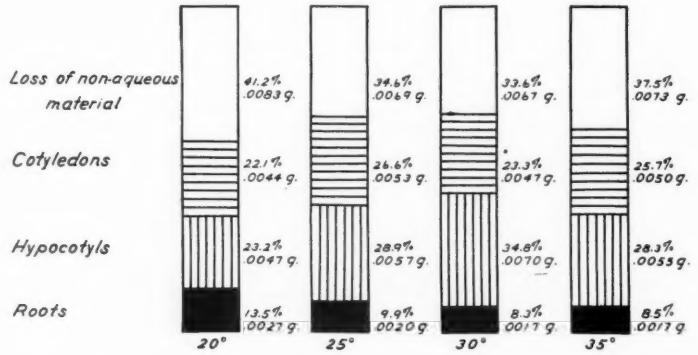


FIG. 4.—Bar diagrams showing relative amounts of dry matter found in cotyledons, hypocotyl, and roots at beginning of death and the proportion used in respiration at four temperatures in the distilled water series.

The seedlings grown on distilled water and agar did not receive any external sources of energy and materials except water and oxygen. Agar is not utilized, as unpublished tests show. As a result the amount of material available for growth and the maintenance of life was restricted to the store of food materials present in the dry seed. In this series the weights may be used directly as an index of the amount of non-aqueous materials remaining at the time of the beginning of death, and they are so treated in the bar diagrams of figure 4. (5) The seedlings grown on Knop's solution were able to absorb salts, and the dry weights represent both non-aqueous organic materials and the unknown amount of salts and so they are of no use in this connection. Dry weights are not available for the distilled water seedlings grown at 15°, unfortunately.

Each seed was weighed individually before planting and the total seed weights used for producing each of the ten experimental groups of seedlings are known. Of the seed weight, 95.49 per cent consisted of non-aqueous materials; and from the dry weights of cotyledons, hypocotyls, and roots the proportions of the original material laid down in these three organs were calculated on a percentage basis. These values are expressed graphically and numerically in figure 4, accompanied by the observed values for dry weights. The sum of the dry weights of the three organs never equaled the original dry seed weight of course; during the life of the plant respiratory processes continually produced water and carbon dioxide, which diffused away, part of their weight probably being compensated for by the weight of the oxygen absorbed. To obtain a measure of the metabolic activity of the seedlings, the total dry weights of the dead plants were subtracted from the calculated dry weights of the seeds used to produce the plants; this quantity is also expressed in figure 4.

The upper sections of the bars, representing the loss in material due to respiratory processes, show a remarkable relationship; the lowest values occur in the optimal temperature range at 25° and 30°. This is remarkable because numerous experimenters working on a variety of kinds of organisms have found that as successively higher temperatures are examined, higher respiratory rates are found; and on that basis one might have predicted that the greatest loss of non-aqueous materials would have been found at the highest rather than at the lowest temperature studied.

WASNIEWSKI'S (7) results on the metabolism of wheat seedlings are of interest in this connection. He grew seedlings to the stage when the third leaf began to unfold at 10°, 20°, and 34° C. on distilled water, Knop's solution, and a N-free salt solution, and made detailed chemical analyses of seeds and seedlings. On the average, about 72 per cent of the starch was used in respiration at 10° and 20° and 82 per cent at 34°, indicating a less economical use of materials above the optimum. Reserve materials were used less economically on distilled water than on Knop's solution by the wheat seedlings. WASNIEWSKI'S experiments were terminated at a much earlier developmental stage than were the present ones.

The highest hypocotyl weights came at 30° and the values for the

other temperatures grade off much as do the heights of the hypocotyl. The root weights were greatest at 20° and decrease with higher temperatures. The bars show that the weights of hypocotyl and roots combined, representing the total production of new tissue, was greatest at 30°. No similar trends are shown by the cotyledons. It appears that the beginning of death found the cotyledons of each group depleted of food materials to about the same extent, both relatively and absolutely.

When the proportions of dry material deposited in the three organs are expressed as percentages of the total dry weight of the seedling (as in table III) instead of on the basis of the original dry weight

TABLE III

PERCENTAGE DISTRIBUTION OF DRY MATERIAL IN PLANTS AT TIME OF BEGINNING OF DEATH; DISTILLED WATER SERIES

PART	20°	25°	30°	35°
Cotyledons	37.6	40.7	35.1	41.1
Hypocotyl	39.5	44.1	52.4	45.2
Roots	22.9	15.2	12.5	13.6
Totals	100.0	100.0	100.0	99.9

of the seed (as in figure 4), very much the same relationships are found.

Except for the entrance of oxygen and the escape of carbon dioxide and water vapor through the cotton stoppers of the tubes, the seedlings were operating in what may be considered to be a closed system; and under the conditions of this experiment the amount of material at the disposal of the embryos was definitely limited to the amount stored in them and in their cotyledons. This material was used almost exclusively, one may suppose, in three ways: for the production of a root system, for the production of a hypocotyl, and expended in respiration. If one selects a set of environmental conditions in which one of these processes is accelerated, it is clear that this can occur only at the expense of one or both of the other processes, provided that the same absolute amount of material in total is taken in each and every case from the available cotyledonary store, under all

of the tested experimental conditions, as appears to have been the case in the present experiments. This principle was expressed in 1822 by GEOFFROY (**2**, p. xxxiii) who wrote, "an organ, normal or pathologic, never acquires an unusual prosperity without a related organ, or one in the same system, suffering for it." The matter can be stated in the opposite way, also. If one selects environmental conditions such that one of these processes is inhibited, then the amount of material available for the remaining processes is conserved and they would appear to have been stimulated. In this sort of system one cannot stimulate or inhibit one function of the organism separately without effect on the others; by choice of suitable temperature and kind of nutrition one can shift the balance of the three major food-consuming processes in this way or that. If temperature is the means used for creating environmental differences in a series of experiments, by this means shifting the internal balance of physiological processes, it is possible to speak of one temperature or another as being optimal; it all depends upon the process being studied.

Another means of altering the balance of physiological processes is illustrated by these data. If nutrient salts are supplied to the seedlings, hypocotyl growth is accelerated, relative to the performance on distilled water, but it is accomplished at the expense of root growth.

DURATION OF LIFE AND RATE OF LIVING

Three types of experiments have shown an inverse relation between growth rate and duration of life in seedlings grown under the same conditions as these.

1. Taking the normal variation in growth rates and in durations of life existing in series of 46 seedlings exposed to the same environmental conditions, PEARL (**3**) worked out the coefficient of correlation, finding it to be, in two different experiments, $-0.463 \pm .078$ and $-0.643 \pm .057$ respectively, indicating that high growth rates are associated to a statistically significant degree with short durations of life. From the results of experiments on *Drosophila* and from consideration of the literature there reviewed, PEARL was led to the conclusion that "in general, the duration of life varies inversely as the rate of energy expenditure during its continuance. In short, the length of life depends inversely on the rate of living."

2. PEARL, EDWARDS, WINSOR, and WINSOR (5) found that when differences in growth were created in *Cucumis* seedlings by differences in aeration, the same relation between growth rate and life duration appeared.

3. In experiments similar to those reported here but conducted with *Celosia cristata* seedlings, EDWARDS, PEARL, and GOULD (1)

TABLE IV

HYPOCOTYL LENGTH, DURATION OF LIFE, AND GROWTH RATE OF CUCUMIS SEEDLINGS

	TEMPERATURE				
	15°	20°	25°	30°	35°
Distilled water					
Mean hypocotyl height, cm.	4.70 ± .07	10.88 ± .11	15.63 ± .09	16.45 ± .10	8.88 ± .13
Standard deviation	0.40 ± .05	0.77 ± .07	0.64 ± .06	0.75 ± .07	0.93 ± .09
Coefficient of variation	8.51 ± .99	7.05 ± .69	4.06 ± .40	4.56 ± .43	10.49 ± 1.08
Duration of growth, days	40	20	15	15	14
Duration of intermediate period	41	30.6	18.3	11.7	16.6
Duration of life, days	81	50.6	33.3	26.7	30.6
Mean growth rate, cm./day	0.118	0.544	1.042	1.097	0.634
Number of seedlings	17	24	24	26	22
Knop's solution					
Mean hypocotyl height, cm.	8.04 ± .11	17.08 ± .17	18.68 ± .17	23.10 ± .20	19.72 ± .16
Standard deviation	0.73 ± .07	1.13 ± .12	1.12 ± .12	1.36 ± .14	1.18 ± .11
Coefficient of variation	9.04 ± .95	6.61 ± .69	5.99 ± .64	5.90 ± .62	5.98 ± .57
Duration of growth, days	34	17	13	11	14
Duration of intermediate period	19.4	17.4	11.8	7.2	3.9
Duration of life, days	53.4	34.4	24.8	18.2	17.9
Mean growth rate, cm./day	0.237	1.005	1.437	2.100	1.409
Number of seedlings	21	21	20	21	25

found considerable differences in growth rate among six temperatures tested, but in general high growth rates were accompanied by short life durations, and slow growth at the low temperatures was followed by long life.

Table IV and figure 5 show the interrelationship of these two functions in the set of data under discussion here. The growth rates have been obtained by dividing the final height in cm. by the duration of

the growth period in days. In the mineral nutrient series the values increase to a maximum at 30°, as was reported previously for this species by PEARL, EDWARDS, and MINER (4), who have discussed this method of calculating the mean growth rate in comparison with other measures. In the distilled water series the rates at 25° and 30° are practically the same and they are higher than at the other temperatures. For comparison with this there are two measures of life duration: (1) the period from planting to the beginning of death, which is greatest at the lowest temperature tested and decreases in

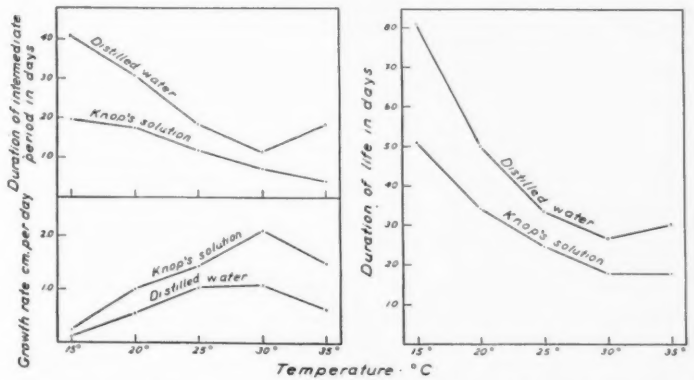


FIG. 5.—Total duration of life, duration of intermediate period, and mean growth rates of *Cucumis* seedlings.

both series to low values for the highest temperatures. (It appears that seedlings lived a little longer at 35° than at 30° on distilled water, but no great importance can be attached to this on the basis of the data available at present.) (2) Since the growth period makes up a substantial part of the total duration of life, the growth rate and total duration of life are not independent variables, arithmetically. Consequently, as in the other papers from this laboratory already referred to, the length of the growth period was subtracted from the duration of life to give the length of time during which the seedlings maintain themselves in an apparently healthy condition but without further change in size (referred to here as the intermediate period). These data fully confirm the conclusions drawn from the earlier ex-

periments in showing an inverse relation between growth rate and life duration.

The two environmental conditions used here as independent variables, namely temperature and nutrition, influence both growth rate and life duration. In general, high temperatures accelerate growth in both series and they shorten life. The addition of salts to the agar also accelerates hypocotyl growth at all temperatures to about twice the rates on distilled water, but the duration of life is reduced at all temperatures also.

This study of the behavior of *Cucumis* seedlings has included only the most easily measured characters, but the observations show that the logically separable functions of the plant, such as hypocotyl growth, or life duration, cannot be altered by suitable choice of environmental conditions without modifying the other activities of the organism also; and in the system set up here one function can be accelerated only at the expense of a complementary function.

Summary

1. *Cucumis melo* seedlings were grown under aseptic conditions on distilled water or on Knop's solution at five constant temperatures between 15° and 35° C., and measurements were made on (1) growth of the hypocotyl, which was found to be greatest and most rapid at 30°; (2) duration of life, which was found to be inversely proportional to temperature; and (3) dry weights of cotyledons, hypocotyl, and roots at the beginning of death.

2. The differences between hypocotyl growth on nutrient and on plain agar were greatest at the temperature extremes and least in the optimal temperature range.

3. The greatest hypocotyl growth occurred on Knop's solution but root growth was poor, compared with distilled water; the optimal temperature for hypocotyl growth was 30°, for roots 15° or 20°; rapid growth was followed by short life duration.

4. In the ten sets of environmental conditions, roots and hypocotyls had different degrees of development and the amount of nonaqueous materials lost in respiration during the life of the plant dif-

fered also. It appears that these processes are so interrelated that any excessive development of one function is counterbalanced by a reduced activity of another function.

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LITERATURE CITED

1. EDWARDS, T. I., PEARL, R., and GOULD, S. A., The growth and duration of life of *Celosia cristata* seedlings at different temperatures. Jour. Gen. Physiol. **17**: July, 1934.
2. GEOFFROY, SAINT-HILAIRE, Philosophie Anatomique. Tome II. pp. xxxiv+550. Paris. 1822.
3. PEARL, R., The rate of living. Alfred A. Knopf, New York. 1928.
4. PEARL, R., EDWARDS, T. I., and MINER, J. R., The growth of *Cucumis melo* seedlings at different temperatures. Jour. Gen. Physiol. **17**:687–700. 1934.
5. PEARL, R., EDWARDS, T. I., WINSOR, A. A., and WINSOR, C. P., Aeration and growth of canteloup seedlings (*Cucumis melo*). Amer. Jour. Bot. **21**:242–250. 1934.
6. TOMKINS, R. G., Studies of the growth of molds. Proc. Roy. Soc. London B. **105**:375–401. 1929.
7. WASNIEWSKI, S., Der Einfluss der Temperatur, des Lichtes und der Ernährung mit Stickstoff und Mineralstoffen auf den Stoffwechsel in den Keimpflanzen des Weizens. Bull. Intern. Acad. Sci. Cracovie. Cl. math.-nat. Serie B. **1914**:615–686. 1917.

SOME NEW OR OTHERWISE NOTEWORTHY MEMBERS OF THE FAMILIES LABIATAE AND COMPOSITAE

EARL EDWARD SHERFF

Haplostachys linearifolia (Dr. del Cast.) comb. nov.— *Phyllostegia linearifolia* Dr. del Cast. Illustr. Fl. Ins. Mar. Pac. 47, *tab.* XX. 1886.

HAPLOSTACHYS LINEARIFOLIA var. **rosmarinifolia** (Hillebr.) comb. nov.— *H. rosmarinifolia* Hillebr. Fl. Haw. Isls. 347. 1888.[1]

Differs from the species proper in having narrower, more elongate-acute calyx lobes, these averaging 2–3.3 mm. rather than 1–1.5 mm. long.

Phyllostegia mannii nom. nov.—*Stenogyne parviflora* H. Mann, Proc. Amer. Acad. **7**:193 (Enum. Haw. Pl. no. 357). 1867.—Very properly regarded by HILLEBRAND (Fl. Haw. Isls. 353. 1888) as a *Phyllostegia*, but confused by him with *P. racemosa* Benth., a quite different species from the Islands of Hawaii and Molokai. *P. mannii* is known only from the Island of Maui. The lower lip of the corolla exceeds the upper, as in other true species of *Phyllostegia*.

PHYLLOSTEGIA GLABRA var. **macraei** (Benth.) comb. nov.— *P. macraei* Benth., DC. Prodr. **12**:554. 1848; *P. glabra* var. *β*. Hillebr. Fl. Haw. Isls. 351. 1888.

PHYLLOSTEGIA GLABRA **lanaiensis** var. nov.—Folia angustiora late oblongo-lanceolata, sub 4 cm. lata, subobscure serrata, sicca subnigrescentia. Calyces ad anthesin obconici (lobis acriter subulatis irregulariter usque ad 7 mm. longis inclusis) circ. 1–1.1 cm. longi; corollis circ. 1.5–1.7 cm. longis, tubo paulo exserto.

Specimens examined: *Mr. Ballieu*, Hawaiian Isls. (Herb. Par.); *George C. Munro*, Isl. Lanai, June 20, 1914 (Herb. U.S. Nat.); *H. Mann* and *W. T. Brigham* 354, Isl. Lanai (type, Herb. Field Mus.).

PHYLLOSTEGIA MACROPHYLLA **remyi** var. nov.—Folia glabriuscula vel moderate adpresso-hispida. Calyces floriferi tantum circ. 2.5 mm.

[1] *Phyllostegia rosmarinifolia* H. Mann, Mem. Bost. Soc. Nat. Hist. **1**:536. 1869 (*nom. nudum*) evidently belongs either to this variety or to the species proper.

longi, lobis sub 0.5 mm. longis, pedicellis 6–8 mm. longis, corollis minoribus vix 1 cm. longis.

Specimens examined: *Jules Remy* 386, Isl. Maui, 1851–1855 (type, Herb. Gray: cotype, Herb. Par.).

PHYLLOSTEGIA MACROPHYLLA **phytolaccoides** var. nov.—Inflorescentia angustior elongatiorque fructifera tantum circ. 1.3–1.7 cm. crassa, verticillastris 6-floris.

Specimens examined: *A. S. Hitchcock* 14897, alt. 4000 ft., in very wet forest along pipe line, east of Olinda, East Maui, Oct. 1, 1916 (type, Herb. U.S. Nat.).

PHYLLOSTEGIA MACROPHYLLA **velutina** var. nov.—Valde sericeo-villiosa vel demum velutina calysis circ. 6–7 mm. longi lobis acutis 2–3 mm. longis, corollae tubo 8–12 mm. longo.

Specimens examined: *U.S.S. Pacif. Explor. Exped. under Capt. Wilkes*, Mauna Kea, Isl. Hawaii, 1840 (type, Herb. U.S. Nat.).

Phyllostegia lantanoides sp. nov.—Suffrutescens, ±4 dm. alta, caule ramisque minutissime glandulosis nodis perspicue retrorsumque nitido-setosis aliter nunc brevissime pubescentibus nunc glabratis. Folia opposita indivisa petiolo perspicue nitido-ciliato 1–2.8 cm. longo, lamina membranacea oblongo-ovata basi truncata vel subcordata apice acuta vel vix acuminata margine crenato-serrata utrinque minutissime numerosissimeque resinoso-glandulosa supra adpresso-hispidula infra non nisi ad venas hispidula 3–6.5 cm. longa et 1.7–3 cm. lata, interdum rugosa. Inflorescentia simplex spicato-racemosa, verticillastris paucis (circ. 4–6) 4- vel 6-floris, bracteis imis foliaceis ±2.5 cm. longis aliis gradatim minoribus ovatis subsessilibus basim versus albo-ciliatis. Calyx obconicus ±4.5 mm. longus resinoso-glandulosus minutissime pubescens subacriter dentatus pedicella ±1.5 mm. longa. Corolla alba vel punicea extrinsecus glanduloso-pubescens circ. 1 cm. longa labio superiore quam inferiore circ. 0.6–0.65 breviore, filamentis pubescentibus, achaeniis triangulatis obovatis apice subtruncatis circ. 2–2.3 mm. longis.

Specimens examined: *Anon.*, Hawaiian Isls. (Herb. Kew); *H. Mann* and *W. T. Brigham*, Kaala Mts., Isl. Oahu (type, Herb. Cornell Univ.).

Phyllostegia bracteata sp. nov.—Subherbacea scandens omnino molliter pubescens caulis ramorumque pilis plerumque retrorsis.

Folia opposita simplicia petiolo tenui 2–4 cm. longo lamina tenera ovata basi truncata vel subcordata apice subacuta margine crenata utrinque resinoso-glandulosa usque ad 5.5 cm. longa et 3.8 cm. lata. Inflorescentia simplex elongate racemoso-spicata 1.5–2.2 cm. longa, verticillastris saepius 8–12, remotis et plerumque 6-floris, bracteis imis foliaceis sub 3 cm. longis aliis rotundato-ovatis stipitatis calycem superantibus. Calyx breviter pedicellatus pedicella sub 2 mm. obconicus vel demum hemisphaericus circ. 3.5 mm. longus apud pilos resinoso-glandulosus acriter dentatus dentibus sub 1 mm. Corolla parva circ. 9 mm. longa extrinsecus pubescens, labio inferiore paulo longiore, filamentis fere glabratis, achaeniis obovatis plano-convexis alatis atris 1.7–2.4 mm. longis.

Specimens examined: *A. S. Hitchcock* 14746, alt. 4000–5000 ft., vine in upper forest, Puu Kukui, West Maui, Sept. 24–26, 1916 (Herb. U.S. Nat., type); *H. Mann* and *W. T. Brigham* 415, West Maui (Herb. Gray; Herb. Mo. Bot. Gard.).

Phyllostegia helleri sp. nov.—Forsitan erecta. Folia ovato-cordata, breviter acuminata, crenato-serrata, laminis pilosis 8–10 cm. longis et 4–6.5 cm. latis, petiolis pilosis 2.5–4 cm. longis. Verticillastra 6-flora in racemis ramosis disposita, bracteis ovatis 3–4 mm. longis. Calyces glanduloso-pubescentes floriferi obconico-campanulati 4–5 mm. longi lobis subacutis circ. 1 mm. longis, fructiferi globoso-obconici, pedicellis subaequalibus. Corollae albae, pubescentes, circ. 1.2 cm. longae, tubo circ. 6–7 mm. longo.

Specimens examined: *A. A. Heller* 2875, on Kaholuamanoa, above Waimea, Isl. Kauai, Oct. 12, 1895 (type, Herb. U.S. Nat.: cotypes, Herb. Field Mus.; Herb. N.Y. Bot. Gard.); *A. S. Hitchcock* 15367, alt. 3600 ft., Kaholuamano, Isl. Kauai, Oct. 20, 1916 (Herb. U.S. Nat.).

PHYLLOSTEGIA PARVIFLORA var. **honolulensis** (Wawra) comb. nov.—*Phyllostegia honolulensis* Wawra, Flora **55**:531. 1872; *ibid.* **58**:286. 1875.

PHYLLOSTEGIA BREVIDENS **pubescens** var. nov.—A specie calycibus pedicellis foliorumque faciebus inferioribus dense pubescentibus caulibus moderate pilosis corollis minoribus 1.6–1.9 non 2.5–3 cm. longis lobis calycinis acutis differt.

Specimens examined: *Rev. J. M. Lydgate*, Upper Kula, Isl. Maui (type, Herb. Berl.).

PHYLLOSTEGIA BREVIDENS **pauciflora** var. nov.—A specie foliis (utrinque) et caulibus pubescentibus verticillastris 6-floris pedicellis (paulo longioribus, saepius 1.4–1.8 cm.) calycibusque pubescentibus lobis calycinis acutis differt; corollis ignotis.

Specimens examined: *Dr. William Hillebrand*, South Haleakala, Isl. Maui, September, 1870 (type, Herb. Berl.).

PHYLLOSTEGIA BREVIDENS **expansa** var. nov.—Folia demum sparsissime caules sparsim pilosa, verticillastris 6-floris, calycibus pedicellisque pubescentibus lobis calycinis fere subulatis, corollis circ. 3 cm. longis extrinsecus manifeste pubescentibus labio plus expanso 1.5–1.8 cm. longo lobo mediano emarginato.

Specimens examined: *Dr. William Hillebrand*, Puu Kukui, West Maui (type, Herb. Berl.).

Phyllostegia rockii sp. nov.—*Phyllostegia hispida* var. β. Hillebr. Fl. Haw. Isls. 353. 1888.—Named for JOSEPH F. ROCK, who collected material of this form at Ukulele, Haleakala, East Maui and proposed it (*in* Herb. Berl.) as a distinct species.

Phyllostegia wawrana sp. nov. (sect. Lateriflorae A. Gray).—Omnino hirsuta, pilis mollibus patentibusque; forsitan herbacea. Folia magna inflorescentiam laminae longitudine superantia, longe petiolata petiolis usque ad 1 dm. longis, lamina membranaceissima suboblongo-ovata subcrenato-serrata serraturis ad unicum latus ±45 basi subcordata apice breviter acuminata usque ad 2 dm. longa et 1.1 dm. lata. Racemi axillares, decompositi (3-partiti), verticillastris numerosis plerumque 6-floris; bracteis ovatis ±4 mm. longis; pedicellis circ. 8–9 mm. longis; calycibus ad anthesin obconicis et circ. 5 mm. longis fructiferis subglobosis et circ. 4–5 mm. crassis lobis acutis 1–2 mm. longis; corollis sub 1 cm. longis labio superiore brevissimo (circ. 2 mm. longo).

Specimens examined: *Dr. Heinrich Wawra* 2060*a*, Isl. Kauai, 1868–1871 (2 type sheets, Herb. Mus. Vienna).

STENOGYNE KAMEHAMEHAE **albiflora** var. nov.—A specie corollis albis vel flavido-albis (nec vel aegerrime coccineo-purpurascentibus) differt.

Specimens examined: *A. S. Hitchcock* 14850, alt. 3000–5000 ft.,

Puu Kukui, West Maui, Sept. 24–26, 1916 (Herb. U.S. Nat.; *forma nonnullis corollis aegre subpurpurascentibus*); *idem* 14894, alt. 4000 ft., very wet forest along pipe line, east of Olinda, East Maui, Oct. 1, 1916 (Herb. U.S. Nat.); *Joseph F. Rock*, Honomanu, East Maui, May, 1911 (Herb. Gray); *idem*, Honomanui Gulch, East Maui, May, 1911 (Herb. Gray); *idem* 8549, trailing over a tree, Pohakumoa Gulch, halfway between Waikamoi and Honomanu Forest of Hamakua, East Maui, September, 1910 (type, Herb. Gray).

Here clearly belongs *Phyllostegia longiflora* Caum (Occas. Paps. Bish. Mus. **9**: (5), 9, pl. 6. 1930), based on *Lyon* and *Caum* 150, a lone plant found along the Kula Pipe Line Trail in East Maui, and "noticeable by its conspicuous large white flowers." *Stenogyne longiflora* Dr. del Cast. (Illustr. Fl. Ins. Mar. Pacif. 57, *tab.* XXVII. 1886), based on *Remy* 379 from Maui, may likewise belong here, rather than with *S. kamehamehae* proper, although DRAKE DEL CASTILLO'S failure to describe the corolla color leaves the identity in doubt. His type seems no longer extant and his plate, uncolored as it is, affords of course no aid as to the corolla-color character.

STENOGYNE SCROPHULARIOIDES **skottsbergii** var. nov.—Folia saepius oblongo-lanceolata rarius ovata, calycis lobis acutis.

Specimens examined: *Charles Gaudichaud*, Hawaiian Isls. (type, Herb. Berl.); *Archibald Menzies*, Hawaiian Isls. (Herb. Kew).

Named for DR. CARL SKOTTSBERG, who had studied the type in 1933 and referred it to *S. scrophularioides* Benth. BENTHAM'S original description (Bot. Reg. **15**: no. 1292, *sub Tribo* 6. Prasieae. 1830), however, was based on *Macrae's* plant, *with obtuse calyx-lobes*.

STENOGYNE SCROPHULARIOIDES **remyi** var. nov.—Folia majora, petiolis sparsissime hispidis 1–1.5 cm. longis, laminis subglabris 5–6 cm. longis et 2.5–3.3 cm. latis, dentibus acrioribus breviter mucronulatis. Verticillastra 6-flora, calycibus acerrime lobatis circ. 7 mm. longis corollae circ. 2.5 cm. longis infra glabratis supra pubescentibus, pedicellis fructiferis 6–12 mm. longis.

Specimens examined: *Jules Remy* 376, Isl. Hawaii (type, Herb. Gray).

STENOGYNE MACRANTHA **gracilis** var. nov.—Suffruticosa, scandens, ramis elongatis gracilibus glabratis, internodiis saepe 8–10 cm. longis. Folia oblonga vel ovato-oblonga, basi truncato-rotundata apice breviter acuminata petiolis 1–2.5 cm. longis laminis 6–7.5 cm.

longis et 2.7–4 cm. latis membranaceis glabratis pallidis. Verticillastra 6- vel interdum 4-flora, pedicellis fructiferis 1–1.5 cm longis, calycibus campanulatis glabratis acriter irregulariterque lobatis (lobis 2–5 mm. longis inclusis) 6–7 rarius usque ad 9 mm. longis, corollis (siccis) flavido-albis infra forsitan aegre coloratis extrinsecus valde sericeis gutture valde ampliatis circ. 2 cm. longis labio inferiore quam superiore multo breviore, filamentis pilosis.

Specimens examined: *Joseph F. Rock* 10037, Hawaiian Isls. (2 type sheets, Herb. Gray).

STENOGYNE MACRANTHA var. GRACILIS **hispida** f. nov.—Caules ramique plus minusve retrorso-hispidi, internodiis paulo brevioribus, foliis viridibus saepe subrugosis infra saepe venosioribus. Calyces fructiferi 1–1.2 cm. longi pedicellis fere aequales. Corollae angustiores, 2.5–3 cm. longae.

Specimens examined: *Joseph F. Rock* 3511, Puulaalaau, west slope of Hualalai, Isl. Hawaii, June 10, 1909 (type, Herb. Gray); *idem* 3513, *eodem loco* (Herb. Gray).

STENOGYNE ANGUSTIFOLIA var. **hillebrandii** nom. nov.—*Stenogyne angustifolia* var. γ. Hillebr. Fl. Haw. Isls. 357. 1888.

STENOGYNE ANGUSTIFOLIA var. **mauiensis** nom. nov.—*Stenogyne angustifolia* var. β. Hillebr. *loc. cit.*

STENOGYNE ANGUSTIFOLIA **spathulata** var. nov.—Folia spathulata, apice subobtusa margine subvaldius serrata, petiolo adjecto 3–4.5 cm. longa et 7–9 mm. lata. Calyces minores 8–10 mm. longi, ad anthesin quam corollae circ. 0.65 (non circ. 0.5) breviores, bracteolis minutis ±3 mm. longis.

Specimens examined: *Jules Remy* 393, Isl. Hawaii, 1851–1855 (type, Herb. Gray).

STENOGYNE ANGUSTIFOLIA **salicifolia** var. nov.—Folia lineari-lanceolata, apice sensim basi sensim vel subabrupte angustata margine subobscure serrata, petiolo adjecto 7–8 cm. longa et 0.9–1.2 cm. lata. Calyces ±1.5 cm. longi, quam corollae circ. 0.4 breviores, bracteolis perspicuis circ. 1 cm. longis.

Specimens examined: *Dr. William Hillebrand*, Isl. Hawaii (type, Herb. U.S. Nat.).

STENOGYNE RUGOSA **mollis** var. nov.—Pube brevi molli induta, ramis saepe elongatis nodis remotis, verticillastris 6–10-floris.

Specimens examined:[2] *Dr. William Hillebrand* 347, Isl. Hawaii (Herb. Gray); *H. Mann* and *W. T. Brigham* 295, woods at base of Mauna Kea, Isl. Hawaii (Herb. Gray); *United States South Pacific Exploring Expedition under Capt. Wilkes*, District of Waimea, Isl. Hawaii, 1840 (type, Herb. U.S. Nat.: cotype, Herb. Gray).

ASA GRAY (Proc. Amer. Acad. **5**:348. 1862) presented a disposition of three sets of variants of *Stenogyne rugosa* Benth., without attempting the use of conventional varietal names. My recent study of a considerable amount of *S. rugosa* material showed the species proper to be highly polymorphic and to consist of the first two sets of variants described by GRAY. His third set, however, is very distinct varietally and well deserves the recognition here accorded it.[3]

STENOGYNE PURPUREA **leptophylla** var. nov.—A specie foliis lanceolatis vel anguste oblongo-lanceolatis (nec ovato-lanceolatis) plerumque sub 7 cm. longis et sub 1.8 cm. latis differt.

Specimens examined: *Joseph F. Rock* 5744, Hawaiian Isls. (Herb. Gray); *idem* 8863, Keaku stream, high plateau of Isl. Kauai, Oct. 21, 1911 (type, Herb. Gray).

STENOGYNE RUGOSA **subulata** var. nov.—Folia laminis sub 6 cm. longa et 2 cm. lata. Calycis lobi acerrime subulati, tubo longiores.

Specimens examined: *Dr. William Hillebrand*, between Kilauea and Kapapala, Isl. Hawaii (type, Herb. Berl.).

Stenogyne calycosa sp. nov.—*Stenogyne sessilis* var. γ. Hillebr. Fl. Haw. Isls. 359. 1888.

STENOGYNE SESSILIS **hexantha** var. nov.—Folia plerumque breviter petiolata petiolis 2–5 mm. longis. Verticillastra principalia 6-superiora 2–4-flora; calycibus ad anthesin circ. 8 mm. longis, lobis acutis; corollis circ. 2.2 cm. longis.

Specimens examined: *Joseph F. Rock* 10036, Hawaiian Isls. (2 type sheets, Herb. Gray).

STENOGYNE SESSILIS var. **lanaiensis** nom. nov.—*Stenogyne sessilis* var. β. Hillebr. Fl. Haw. Isls. 359. 1888.

Stenogyne sororia sp. nov.—Omnino glaberrima (corollis exclusis), foliis tenuiter petiolatis petiolo sub 1.5 cm. longo lamina simplici membranacea ovata basi subcordata apice breviter acuminata margine remote aegreque denticulata circ. 3.5–4.5 cm. longa.

[2] Only a small proportion of those studied are included here.

[3] HILLEBRAND'S var. and γ (Fl. Haw. Isls. 356. 1888) is identical with this variety.

Verticillastra 6-flora, pedicellis saepius 7–9 mm. longis, calycibus obconicis (dentibus magnis acerrimis adjectis) 1.2–1.4 cm. longis; corollis immaturis extrinsecus pubescentibus.—An ally or sister species of *S. scrophularioides* Benth.

Specimens examined: *Dr. William Hillebrand*, Hawaiian Isls. (type, Herb. Kew).

Stenogyne scandens sp. nov.—Subherbacea, scandens vel procumbens, caule ramisque subglabris. Folia petiolata petiolis dorsaliter pubescentibus 5–10 mm. longis, lamina simplici membranacea saepius oblonga rarius lanceolato-oblonga basi truncata vel late cuneata apice obtusa vel rarius subacuta margine plerumque crenulato-dentata raro subacriter dentata supra venis minute hispidula aliter glabra infra praecipue ad venas irregulariter pilosa 2.5–3.5 (rarius –5) cm. longa. Verticillastra 6-flora, pedicellis sparsim pilosis tantum 2–5 mm. longis, calycibus late obconicis sparsissime setosis (lobis lanceolato-linearibus acribus adjectis) 6–8 mm. longis; corollis pallide purpureis extrinsecus valde pubescentibus, ± 1.8 cm. longis, labio inferiore brevissimo, filamentis (unico latere pubescentibus) styloque longe exsertis.—Habitu *Phyllostegiae racemosae* Benth. et *S. vaganti* Hillebr. similis.

Specimens examined: *Dr. William Hillebrand* 352, Isl. Hawaii (type, Herb. Kew: a probable duplicate, Herb. Berl.).

Bidens hivoana Degener & Sherff, sp. nov.—Frutex ramosus, glaber, ± 2 m. altus. Folia opposita, subconferte ad ramuli finem disposita, petiolata petiolis conduplicatis marginatis basi dilatato-connatis 1.5–3 cm. longis, petiolo adjecto circ. 6–8 cm. longa et 2.5–3.8 cm. lata, indivisa, ovata, basi rotundata vel raro vix subcordata, apice subacuta vel subattenuata, membranacea, obsolete ac remote serrulata, eciliata. Capitula terminaliter circ. 3-adgregata, pedunculata pedunculis suberectis glabratis ± 2.5 cm. longis, ut videtur radiata (ligulis in typo non plene cretis), disco ad anthesin circ. 6–7 mm. crasso et circ. 9–11 mm. alta. Involucri glabrati bracteae exteriores circ. 4, ovato-oblongae vel late lanceolatae, obtusae, usque ad 8 mm. longae, quam interiores oblongae paulo longiores. Flores ligulati (fide lectorum descriptionis) albi. Paleae angustissime lineares, usque ad 11 mm. longae. Achaenia submatura plana, oblanceolata vel obovata, atro-brunnea, glabra, apice bidentata dentibus glaberrimis deorsum in margines membranaceas luteo-brunneas alis

similes desinentibus, corpore ± 5.5 mm. longa et marginibus alatis adjectis 2.3–3 mm. lata.

Specimens examined: *Adamson* and *Mumford* 469, growing 2 m. tall, alt. 3620 ft., in typical forest of cloud zone, on crest north of summit of Mt. Temetiu, Tenatinaei, Isl. Hiva Oa, Marquis Isls., Jul. 24, 1929 (type, Herb. N.Y. Bot. Gard.).

Recently Mr. OTTO DEGENER noted two specimens among the newer accessions in the Herbarium of the New York Botanical Garden. These he suspected of being new and had them forwarded to me for study. Each is found to be the type of a new species, bringing the total number of *Bidens* species indigenous to the Marquis Islands up to six. Mr. DEGENER courteously permits the use of his name in joint authorship.

Bidens collina Degener & Sherff, sp. nov.—Frutex erectus, gracilis, ramosus ramis obscurissime adpresso-setosis circa 1 m. altus. Folia opposita, tenuiter petiolata petiolis saepius 1.5–2 cm. longis, petiolo adjecto 5–6 cm. longa et 1.5–3 cm. lata, indivisa, oblongo-lanceolata vel oblongo-ovata, rotundato-truncata vel fere subcordata, apice abrupte attenuata, membranacea, faciebus glabrata, marginibus acriter serrulata (unico latere 8–20-dentata). Capitula corymbose disposita, radiata, pansa ad anthesin 1.3–2 cm. lata et circ. 5 mm. alta. Involucri bracteae hispidae exteriores 5–8, lineares vel oblongae apicem abrupte mucronulatum versus saepe dilatatae, 1.5–3 mm. longae, interioribus lanceolato-oblongis dimidio breviores. Flores ligulati plerumque 5 vel 6, flavi, ligula oblongi vel late oblanceolati, apice 2–3-denticulati, circ. 7–9 mm. longi. Achaenia submatura plana, lineari-oblonga, sursum sensim angustata, faciebus marginibusque perspicue erecto-setosa setis fulvescentibus corpore sub 2.5 mm. longa et sub 0.8 mm. lata, apice erecte setosa setis pluribus (saepe 2 longioribus et aristis non dissimilibus).

Specimens examined: *Adamson* and *Mumford* 400, growing about 1 m. tall on exposed hillside, alt. about 100 m., Tehutu, Isl. Hiva Oa, Marquis Isls., May 19, 1929 (type, Herb. N.Y. Bot. Gard.).

Described by the collectors as rare and unknown to many residents of Hiva Oa.

Bidens onisciformis sp. nov.—Herba, unico ramo viso gracili subtereti sulculato sparsissime piloso internodiis folia superantibus.

Folia opposita tenuiter petiolata petiolo ± 5 mm. longo adjecto sub 3 cm. longa, hispida setis pluriloculatis, bipinnatisecta segmentis ultimis membranaceis plus minusve oblongis acriter apiculatis vel dentatis dentibus vix mucronatis. Capitula pauca, tenuiter pedunculata pedunculis superne hispidis ± 3 cm. longis, ad anthesin cernua circ. 2 cm. lata et circ. 6 mm. alta, disco parvo demum circ. 6–7 mm. crasso. Involucri hispidi bracteae exteriores circ. 8, patentes, lineares, ± 5 mm. longae, quam interiores ovatae saepe paulo longiores. Flores ligulati 6 (pro unico capitulo ad anthesin viso), flavi, ligula elliptico-oblanceolati, apice vix denticulati, 8–10 mm. longi. Paleae lineari-oblongae, apice obtusae vel raro irregulariter mucronatae, circ. 5–5.5 mm. longae. Achaenia exteriora fertilia, obcompressa, moderate vel late oblonga, nigra, dorso ± 8-sulculata et glabrata, marginibus pectinato-dentatis vel laceratis (non vere alatis) sursum albido-setosa, ventro circ. 8-sulculata et valde papillato-setosa setis albis, apice bidenticulata (sed vix aristulata) et erecte setosa, 4–5 mm. longa et 1.5–1.8 mm. lata; interiora sterilia, planiora, elongatiora, angustiora, griseo-nigra.

Specimens examined: *Van den Houdt* 211, alt. about 2200 m., northeastern Belgian Congo, 1932 (type, Herb. Brussels).

The outer achenes offer a strong superficial resemblance to sow bugs, of the genus *Oniscus*, whence the trivial name.[4]

Bidens kivuensis sp. nov.—Herba parce suffruticosa, verisimiliter perennis, ± 2 m. alta, erecte ramosa, caule ramisque subtetragonis sparsissime hispidis setis articulatis. Folia opposita petiolata petiolis tenuibus ± 1.5 cm. longis hispidis setis patentibus pluriloculatis, petiolo adjecto 6–9 cm. longa, 2–3-pinnatisecta, segmentis ultimis lineari- vel lanceolato-oblongis membranaceis supra adpresse infra saepius patente hispidis acriter dentatis dentibus mucronatis sed non in setas productis. Capitula corymbose ad ramorum fines 3–5-adgregata pedicellis tenuibus pilosis setis patentibus subalbis pluriloculatis, radiata, pansa ad anthesin ± 4.5 cm. lata et ± 8 mm. alta. Involucri albido-hispidi bracteae exteriores circ. 8, oblongo-lineares, mediane 1-nervatae nervo atro, apice acutae, circ. 4 mm. longae, quam interiores oblongo-ovatae moderate longiores. Flores

[4] I have taken the name *Oniscus* in its restricted sense as used in modern Latin by zoölogists, rather than from the Greek.

ligulati plerumque 8, flavi, ligula oblanceolate lineari-oblongi, apice integri, ±2.2 cm. longi. Paleae lineari-oblongae, circ. 5–6 mm. longae. Flores tubulosi tubo (ac corollae lobis aurantiacis) sparsim patenti-pilosi. Achaenia matura deficientia. Ovaria plana, linearioblonga, anguste marginata, faciebus marginibusque inferne glabrata superne erecto-setosa, apice erecte setosa et exaristata vel minutissime biaristata aristis glabris.

Specimens examined: *Jean Lebrun* 5467, a somewhat suffrutescent herb ±2 m. high, on savanna at 1720 m. alt., Mulungu, Belgian Congo, May, 1932 (1st and 2nd type sheets, Herb. Bruss.: 3rd type sheet, Herb. Field Mus.).

Referred to *Bidens* with some degree of hesitancy in the absence of mature achenes. Should these prove to be definitely *alate*, a closer affinity with *Coreopsis* would be indicated. In *Bidens* the position occupied is close to *B. grantii* (Oliv.) Sherff, *B. gracilior* (O. Hoffm.) Sherff, *B. taylori* (S. L. Moore) Sherff, *B. elliotii* (S. L. Moore) Sherff, and *B. schlechteri* Sherff.

BIDENS STEPPIA **humbertii** var. nov.—Gracilis, ±1 m. alta, ramis erectis sparsim piloso-hispidis. Achaenia 6–7 mm. longa et circ. 1.7–1.9 mm. lata, exaristata, facie dorsali glabrata ventrali ac marginibus apiceque erecto-setosa.

Specimens examined: *H. Humbert* 7593, alt. 2400–2790 m., Biega Mountains, west of Lake Kivu, eastern Belgian Congo, March, 1929 (type, Herb. Bruss.).

BIDENS GRANTII **scaettae** var. nov.—Gracilis, ±5 dm. alta, caule subsimplici glabrato vel supra sparsim piloso internodiis principalibus quam foliis multo longioribus. Folia breviter petiolata vel subsessilia, ±5 cm. longa, bi-tripinnatisecta, supra moderate infra densissime hispida, lobis lineari-oblongis ultimis acerrime apiculatis terminali 1.5–2 cm. longo et circ. 2–3 mm. lato. Achaenia corpore circ. 4 mm. longa et sub 1 mm. lata, aristis circ. 1.5 mm. longis.

Specimens examined: *H. Scaetta* 2286, Nyabihu, Ruanda District, easternmost Belgian Congo, 1930 (type, Herb. Bruss.); *idem* 2294, on clay soil in field unused for 10 years, dry country, *eodem loco et tempore* (Herb. Bruss.).

Coreopsis curtisii sp. nov.—Herba erecta, verisimiliter perennis, gracilis, forsitan circ. 0.5 m. alta, subsimplex, caule angulato glaber-

rimo plus minusve purpureo-striato. Folia opposita, tenuiter petiolata petiolis glaberrimis basi connatis usque ad 2 cm. longis, petiolo adjecto usque ad 8 cm. longa, pinnata vel bipinnatisecta, laminae circumambitu triangulato-ovata, segmentis primariis pallidis membranaceis lanceolatis acriter dentatis secundum venas marginesque nunc sparsissime nunc subconferte albido-setulosis. Capitula pauca, ±3-adgregata et ad rami finem corymbose disposita pedunculis erectis tenuibus glaberrimis 4-8 cm. longis, radiata, pansa ad anthesin circ. 3–3.5 cm. lata et circ. 11–13 mm. alta. Involucri pallidi bracteae supra reflexae, exteriores circ. 8 vel 9, lineari-oblongae, glabrae vel basi extrema hispidae, apice acutae, ±4 mm. longae, interioribus ovato-oblongis apice glanduloso-pubescentibus moderate breviores. Flores ligulati circ. 8, aurantiaci, ligula anguste oblongi, apice integri vel subdenticulati, ±1.5 cm. longi. Paleae lineari-oblongae, apicem versus valde aurantiacae, apice ipso subobtusae. Flores tubulosi extrinsecus glabrae vel secundum corollae superne aurantiacae dentes pubescentes et ad tubi apicem sparsim pilosi; stylorum ramis pulcherrime aurantiacis et elongato-appendiculatis. Achaenia matura non visa. Ovaria plana, oblanceolata, nitido-brunnea, longitudinaliter pluristriata, plus minusve alata, marginibus et faciebus saltem supra erecte setosa, corpore ±4 mm. longa, apice valde erecto-setosa et biaristata aristis glaberrimis ±1.5 mm. longis.

Specimens examined: *Mrs. Richard C. Curtis*, cultivated in 1930, from seeds obtained in Angola (type, Herb. Field Mus.).

A species offering a superficial resemblance in leaf outline and dissection to *C. oligoflora* Klatt. In the key proposed by me in an earlier article (Bot. Gaz. **91**:314–317. 1931) for identification of the African species of *Coreopsis*, this species would run down to *C. monticola* (p. 316, line 10). The pertinent portion of that key may now be altered to read:

1. Involucrum non nisi basi hispidum
   - m. Caulis rigidus superne circ. 2.5–3.5 mm. crassus, foliis principalibus petiolo adjecto circ. 4–5 cm. longis, capitulis pansis 4–5.5 cm. latis, planta kamerunensi ..... 10. *Coreopsis monticola*
   - m. Caulis gracilis superne 1–2 mm. crassus, foliis principalibus petiolo adjecto 5–8 cm. longis, capitulis pansis 3–3.5 cm. latis, planta angolensi. 17*a*. *Coreopsis curtisii*

Cosmos mattfeldii sp. nov.—Herba perennis (Sectionis *Mesineniae*), gracillima, ± 5 dm. alta, caule subsimplici superne glabro inferne adpresso-hispido setis arcuatis retrorsis ± 1.5 mm. crasso e radice tuberosa. Folia opposita, petiolata petiolis tenuibus sparsissime hispidis et basi plus minusve hispido-ciliatis usque ad 2.5 cm. longis, petiolo adjecto saltem 5–8.5 cm. longa et 0.8–2 cm. lata, simplicia, lamina lanceolata vel ovato-lanceolata, membranacea, faciebus glabra, basi late apice anguste (vel angustissime) cuneata, marginibus minutissime spinuloso-ciliata et pauciter acridentata (unico latere plerumque 3- vel 4-dentata), inferiora quam internodia multo longiora superiora multo breviora. Capitula perpauca (tantum 2 pro unico specimine viso), longissime tenuissimeque pedunculata pedunculo 1.2–2.7 dm. longo et usque ad circ. 1 mm. crasso, radiata, pansa ad anthesin circ. 4.6 cm. lata et circ. 1.2 cm. alta. Involucri bracteae exteriores circ. 8 vel 9, lanceolato-oblongae, glabrae, tergo circ. 5-nerviae, apice attenuatae vel acutae, circ. 8 mm. longae, interioribus ovato-oblongis apice glanduloso-pubescentibus paulo longiores. Flores ligulati 7 forsitan saepius 8, atro-sanguinei, ligula oblanceolato-oblongi, apice subintegri vel irregulariter dentati, ± 2.3 cm. longi. Paleae lineari-oblongae, glabrae, supra sanguineae, apice acutae et disci flores superantes. Flores tubulosi extrinsecus plerumque glaberrimi, superne sanguinei vel purpurascentes. Achaenia matura non visa. Ovaria minuta, obcompressa, faciebus marginibusque glabra, apice biaristata aristis tenuibus retrorsum hamosis 5–6 mm. longis.

Specimens examined: *E. Langlassé* 369, in clay soil, alt. 900 m., La Laja, southern Mexico, Sept. 21, 1898 (type, Herb. Berl.).

Collected the same month and by the same collector as was *C. langlassei*, previously described by me (*cf.* Field Mus. Bot. Ser. 8:425. 1932). The locality, like many other of *Langlassé's* localities, is one absent from the atlases, but the states given on the *Langlassé* labels are Michoacan and Guerrero. The type, along with many other specimens of Compositae, had been obtained for my study from the vast accumulation of undetermined material at Berlin, by Dr. JOHANNES MATTFELD, after whom the species is gratefully named.

Cosmos herzogii sp. nov.—Herba suffruticosa verisimiliter peren-

nis, ramis gracilibus glabris sulculatis inferne subteretibus superne angulatis, caulium glabratorum internodiis inferioribus sub 1 cm. longis. Folia opposita, tenuissime petiolata petiolis 1–2 cm. longis, petiolo adjecto 5–7.5 cm. longa, glaberrima, circumambitu ovato-triangulata, bipinnatisecta, segmentis primariis plerumque 5 membranaceis eciliatis sparsim atro-punctulatis, ultimis lineari-oblongis 2–3 (–5) mm. latis apice acribus margine saepe 1- vel 2-dentatis dentibus acutis. Capitula perpauca vel solitaria ramos terminantia, radiata, pansa ad anthesin circ. 2.5 cm. lata. Involucri bracteae exteriores circ. 8, lineari-attenuatae, glabrae, apice acutae, circ. 6 mm. longae, patentes; interiores lineari-oblongae, marginaliter diaphanae, apice minutissime pubescentes alibi glaberrimae, circ. 7–8 mm. longae. Flores ligulati circ. 8, flavi, ligula lineari-elliptici vel -oblongi, tantum circ. 6- vel 7-nervati, apice integri vel 2-dentati, circ. 1.3–1.5 cm. longi et 3–3.5 mm. lati. Paleae lineari-oblongae, marginibus integrae vel irregulariter acriterque 1–2-dentatae, circ. 7–9 mm. longae. Flores tubulosi extrinsecus sparsim adpresso-pubescentes; stylorum ramis extremo rotundatis abrupte longeque lineari-appendiculatis. Achaenia matura non visa. Ovaria plana vel subplana, cuneato-oblonga, nunc valde nunc aegre hispida, corpore circ. 1.5 mm. longa, apice 2- vel irregulariter 3-aristata aristis retrorsum 1–3-hamosis sub 0.5 mm. longis.

Specimens examined: *Theodor Herzog* 496, an abundant "half-shrub" ("Halbstrauch") on sandstone, alt. about 900 m., summit of Cerro San Miserate, Chiquitos, Department of Santa Cruz, Bolivia, May, 1907 (type, Herb. Berl.).

In leaf outline superficially resembling the purplish-rayed *C. peucedanifolius* of the Section *Discopoda*, but in characters of the capitula much closer to *C. langlassei* of the Section *Mesinenia*. Achenes and roots are much to be desired.

×**Dubautia fucosa** hybr. nov.—Rami (ramuli?) graciles, infra glabrati et moderate vel confertissime foliosi, supra hispiduli et subnudi. Folia opposita vel superiora alterna, plus minusve demissa, revoluta, linearia vel anguste lanceolato-linearia, basi subangustata marginataque, apice acriter attenuata, glaberrima, subcoriacea, apicem versus utroque latere minute 1–4-denticulata, manifeste 3- vel sub-5-nervia, 4.5–6.5 cm. longa et 3–5 mm. lata. Paniculae ramis

principalibus alternis et capitulorum notis *Dubautiae plantagineae* ipsi nisi pappo interdum paululum plumosiore valde similis. Achaenia fertilia.

Specimens examined: *Rev. J. M. Lydgate*, Isl. Lanai, Hawaiian Isls. (type, Herb. Berl.).

An undoubted hybrid. The inflorescence is that of *Dubautia plantaginea* proper, although the pappus is slightly more plumose than in that species and approaches that of *Railliardia*. The foliar habit, however, is quite unlike that of any *Dubautia* species but is much the same as that found regularly or at times in *Railliardia scabra* var. *leiophylla*, *R. coriacea*, *R. demissa*, and ×*Dubautia fallax*. The type was formerly in HILLEBRAND'S private herbarium and by him had been determined as *Railliardia molokaiensis* (for which *cf.* his citation of "Lanai," Fl. Haw. Isls. 226. 1888). From a consideration of geographic distribution, this hybrid would seem to be *Dubautia plantaginea*×*Railliardia scabra* var. *leiophylla*.

×**Dubautia fallax** hybr. nov.—Rami hispidi, 2–4 dm. longi. Folia inferiora saepe confertissima demissaque superiora laxe disposita, lineari-lanceolata, apice acuta vel subattenuata, glaberrima, coriacea, utroque latere 1–6-denticulata, 3–8 cm. longa et 5–8 mm. lata. Inflorescentia *Railliardiae demissifoliae* et *R. thyrsiflorae* similis sed achaeniis sterilis et pappo prope *Dubautiam*.

Specimens examined: *Otto Degener* 4242, on rain- and fog-swept lava flow at top of Koolau Gap, within Haleakala Crater, Isl. Maui, Hawaiian Isls., Aug. 17, 1927 (Herb. Brit. Mus.; Herb. Field Mus.; Herb. N.Y. Bot. Gard.); *idem* 4273*b*, *eodem loco*, Aug. 11, 1927 (Herb. Berl.; Herb. Brit. Mus.; Herb. Deless.; Herb. Field Mus.; Herb. Gray; Herb. Mo. Bot. Gard.; Herb. N.Y. Bot. Gard.; Herb. Par.; Herb. U.S. Nat.; *cum Railliardia demissifolia et R. thyrsiflora commixta*); *Albert S. Hitchcock* 14955, alt. 6000–10000 ft., on rocky slope of Haleakala Crater, Isl. Maui, Oct. 2–5, 1916 (type, Herb. U.S. Nat.).

On comparison with the somewhat similarly leaved hybrid *Railliardia fucosa*, the inflorescence and habitat of which betray *Dubautia plantaginea* as indisputably one of the parents, ×*D. fallax* seems to be likewise a derivative from *D. plantaginea* in part or rather from a variety of *D. plantaginea*, since that species itself is known only from

Lanai. The shortly ciliate pappus bristles are, moreover, characteristic of *Dubautia*. In most characters of the inflorescence it is near to *R. demissifolia* and *R. thyrsiflora*, with which two species it was found by *Degener* to be growing intermixed.

DUBAUTIA LAXA **blakei** Degener & Sherff, var. nov.—Folia linearia vel anguste oblanceolata, apice acriter attenuata, acute sed pauciter spinuloso-denticulata, glabra sed saepe ciliata ac minutissime glandulosa plus minusve 3–5-(sub-7-) nervia. Involucri bracteae extrinsecus glabratae vel sparsim hispidae.

Specimens examined: *Otto Degener* 4234, in windy rain forest, ridge north of Pohakea Gulch, Isl. Maui, Hawaiian Isls., Jul. 23, 1927 (3 type sheets, Herb. Field Mus.: cotypes, Herb. Berl.; Herb. Boiss.; Herb. Brit. Mus.; Herb. Univ. Calif.; Herb. Deless.; Herb. Gray; Herb. Kew; Herb. Mo. Bot. Gard.; Herb. Mus. Vienna; Herb. N.Y. Bot. Gard.; Herb. Par.; Herb. Phila.; Herb. U.S. Nat.; Herb. Univ. Vienna).

Named for Dr. SIDNEY F. BLAKE, who had made a preliminary study of various species of *Dubautia* and *Railliardia* and had recognized this as new.

DUBAUTIA LAXA **waianensis** Degener & Sherff, var. nov.—Folia oblonge obovata vel ovata, apicem obtusum vel abrupte acutum versus minutissime denticulata, utrinque subadpresse papillato-hispida, usque ad 5.5 cm. longa et 2.2 cm. lata. Inflorescentia corymbosa, laxior, pedicellis tenuibus pilosis suberectis saepe 1–2 cm. longis. Involucri bracteae extrinsecus hispidae.

Specimens examined: *Otto Degener* and *K. K. Park* 4327, about 3–5 ft. tall, along summit ridge, between Puu Manawahua and Palikea, Isl. Oahu, Sept. 27, 1931 (Herb. Brit. Mus.; Herb. Deless.; Herb. Field Mus.; Herb. Gray; Herb. Kew; Herb. Mo. Bot. Gard.; Herb. N.Y. Bot. Gard.); *Kazuto Nitta* (*Otto Degener* distrib. no. 4340), alt. 2500 ft., in moderately wet locality, Mt. Kaala, Waianae Range, Isl. Oahu, Hawaiian Isls., 1929 (type, Herb. Field Mus.: cotype, Herb. N.Y. Bot. Gard.).

DUBAUTIA KNUDSENII **degeneri** var. nov.—Frutex ± 1.5 m. altus, ramulis hispidis. Folia obovata, sicca brunneo-viridia, distincte 5-nervia, subsparsim ciliata, inferne praecipue secundum venas plus minusve hispida.

Specimens examined: *Otto Degener* 4259, shrub 5 ft. high, in open rain forest, north of Pepeopae, northeastern Molokai, Hawaiian Isls., May 8, 1928 (type, Herb. Field Mus.); *idem* 4261, in rainy region, on crest of Waikolu Valley, Isl. Molokai, May 1, 1928 (Herb. Field Mus.; Herb. N.Y. Bot. Gard.).

Dubautia paleata×D. waialealae hybr. nov.—Folia conferta internodiis hispidis saepius 2–6 mm. longis, spathulato-oblanceolata, nunc 4–5 cm. longa et 7–12 mm. lata nunc 7–9 cm. longa et 1.2–1.6 cm. lata, apice acuta basi 3–6 mm. lata, utrinque adpresso-hispida. Capitula paniculata vel compacte ac contracto-corymbose disposita, varia sed iis *Dubautiae waialealae* propria.

Specimens examined: *Albert S. Hitchcock* 15468, in bog, alt. 3600–5080 feet, Waialeale, Isl. Kauai, Hawaiian Isls., Oct. 22–24, 1916 (Herb. U.S. Nat.); *idem* 15492, *eodem loco et tempore* (Herb. U.S. Nat.).

Closer to *D. paleata* Gray in size, shape, texture, and arrangement of leaves, but closer to *D. waialealae* Rock in compactness of the inflorescence and most characters of the capitula. The indubitable occurrence of hybridity shown in this case between the bizarre *D. waialealae* and one of the more orthodox species of *Dubautia* is important in that it raises a query as to the integrity of *D. waialealae* var. *megaphylla* Sherff.[5]

×**Railliardia dolosa** Degener & Sherff, hybr. nov.—Folia opposita, patentia vel demissa, oblonge et interdum anguste lanceolata oblanceolatave, sessilia, rigida, apicem acutum versus obsolete serrulata, 5–7-nervia, faciebus glabrata, marginibus ciliata, principalia 3.5–5.5 cm. longa et circ. 1–1.4 cm. lata. Capitula laxe et racemoso-paniculate disposita pedicellis pilosis suberectis saepius 1–3 cm. longis, involucro obconico-campanulato 6–8 mm. alto. Hybrida, probabiliter inter *Railliardiam menziesii* et *R. platyphyllam*.

Specimens examined: *Otto Degener*, Koolau Gap, Haleakala Crater, Isl. Maui, Hawaiian Isls., Aug. 19, 1927 (Herb. Field Mus.); *idem* 4243, tree 10 ft. tall, in rain forest just below summit of Koolau Gap, Aug. 17, 1927 (Herb. Field Mus.; Herb. N.Y. Bot. Gard.); *idem*

[5] The leaves of *D. waialealae* var. *megaphylla* have the appearance of being diminutive, somewhat metamorphosed leaves of *D. plantaginea* Gaud. or one of its several varieties.

4270, sparingly branched shrub about 2–4 ft. tall, found especially on inner slopes of and on driest lava at bottom of Haleakala Crater, Aug. 20, 1927 (Herb. Field Mus.; Herb. N.Y. Bot. Gard.); *idem* 4271, *eodem loco*, near Kaupo Gap, Aug. 20, 1927 (3 type sheets, Herb. Field Mus.: cotypes, Herb. Berl.; Herb. Boiss.; Herb. Brit. Mus.; Herb. Univ. Calif.; Herb. Deless.; Herb. Gray; Herb. Kew; Herb. Mo. Bot. Gard.; Herb. Mus. Vienna; Herb. N.Y. Bot. Gard.; Herb. U.S. Nat.).

×**Railliardia vafra** Degener & Sherff, hybr. nov.—Frutex ±9 dm. altus. Folia opposita, elliptico-oblonga vel lanceolato-oblonga, sessilia, apice subacuta, integra, subcoriacea, plerumque 5-nervia, glabra atque eciliata sed minutissime plus minusve glandulosa, 3–4 cm. longa et 6–10 mm. lata. Inflorescentia capitulorumque notis *Railliardiae lineari* non dissimilis. Hybrida, probabiliter inter *R. linearem* et *R. menziesii*.

Specimens examined: *Everett Brumaghim* (*Otto Degener* distrib. no. 4336), near Kilauea on Kau side, Isl. Hawaii, Hawaiian Isls., October, 1932 (Herb. Field Mus.; Herb. N.Y. Bot. Gard.); *Otto Degener* 2134, a shrub 3 ft. tall, 25 miles from Waimea toward Kona, Pahoehoe Desert, Isl. Hawaii, Aug. 18, 1926 (2 type sheets, Herb. Field Mus.: cotypes, Herb. Berl.; Herb. Brit. Mus.; Herb. Gray; Herb. Kew; Herb. Mo. Bot. Gard.; Herb. N.Y. Bot. Gard.); *idem* 4226, *eodem loco et tempore* (Herb. Field Mus.; Herb. N.Y. Bot. Gard.).

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COMPARATIVE MORPHOLOGY OF DUMORTIERA HIRSUTA

SISTER MARY ELLEN O'HANLON

(WITH THIRTY-FIVE FIGURES)

Introduction

In 1919, EVANS (4) published the results of an investigation on the taxonomy of *Dumortiera*. Owing to the untrustworthy nature and inconstancy of certain differential characters which have been employed by previous writers to define the various species of *Dumortiera*, EVANS concluded that there are but two known species of this genus, *D. hirsuta* and *D. nepalensis*. He bases the specific differences on the general character of the upper surface of the thallus in each species.

The present study was undertaken chiefly to observe the process of spore germination and to compare it with that of some of its congeners, namely, *Marchantia polymorpha* (7), *M. domingensis* (10), *Preissia quadrata* (8), *Conocephalum conicum* (6), and *Reboulia hemisphaerica* (9). The plant material was furnished through the courtesy of Professor HERMAN KURZ, who collected it near Tallahassee, Florida.

CAMPBELL (2) states that *Dumortiera hirsuta* occurs in the British Isles, Japan, and in the southeastern United States. In his study of the East Indian hepatics, he makes reference to *D. trichocephala*. His description of the same species from the Hawaiian Islands is in full agreement with EVANS' key to *D. hirsuta* and also with the results of this study.

Investigation

CARPOCEPHALUM AND SPOROPHYTE

Plants bearing ripe sporophytes reached the laboratory on April 20. Many of the capsules had already begun dehiscence and some of the spores were sown immediately in small glass stender dishes filled with a mineral nutrient solution. These cultures were placed in north, south, and east exposures of the same room. Some of the

carpocephala and pieces of the thalli were killed in chrom-acetic acid solution for a study of the adult plant.

The carpocephalum is borne on a stalk which has two groups of rhizoids on the side which corresponds to the ventral side of the thallus. The archegonia are borne in groups of which eight is probably the average number. Usually one, sometimes two sporophytes come to maturity in each of the groups.

The sporophyte (fig. 1) is made up of the usual parts: foot, seta, and capsule, and seems to resemble in its general structure the sporophyte of *Marchantia* and its nearer relatives more than it does some of the other members of the family. The foot is indistinctly anchor-like; the seta is prominent, massive, and more or less columnar; the capsule is oval in its general contour, with a slight depression at the basal end. The whole is surrounded by a calyptra which is six cells in thickness. The spore output, estimated at 50,000 spores to a capsule, falls short of that of *Marchantia polymorpha* which, with its approximate 300,000 spores, probably reaches the peak of spore production in these hepatics; it exceeds *M. domingensis* with a capsular output of about 20,000 spores; and it still further surpasses in spore production *Preissia* (**8**), *Conocephalum* (**6**), and *Reboulia* (**9**), which with their increased proportionate numbers of elaters and greater spore size have much reduced numbers of spores. The elaters of *D. hirsuta* would be difficult to distinguish from those of *Marchantia* in form, size, and color, and their number in proportion to the spore number is probably about the same as in the case of *M. domingensis* (**1**), that is, 32 or 64 spores to each elater.

Spore germination

The size of the spore of *D. hirsuta*, about 30 μ in its longest axis, is also nearer to that of *M. domingensis* than it is to any of the others with which comparison has been made. The spores, which were sown on a liquid medium, showed signs of germination on the sixth day. This was manifest by their increased size and their extended form. Germination was 100 per cent. The volume of a germinating spore is probably four or more times that of a newly shed spore (figs. 2, 3). In this feature, *Dumortiera* inclines to the condition in *M. polymorpha*, where there is great increase in the spore size prior to germina-

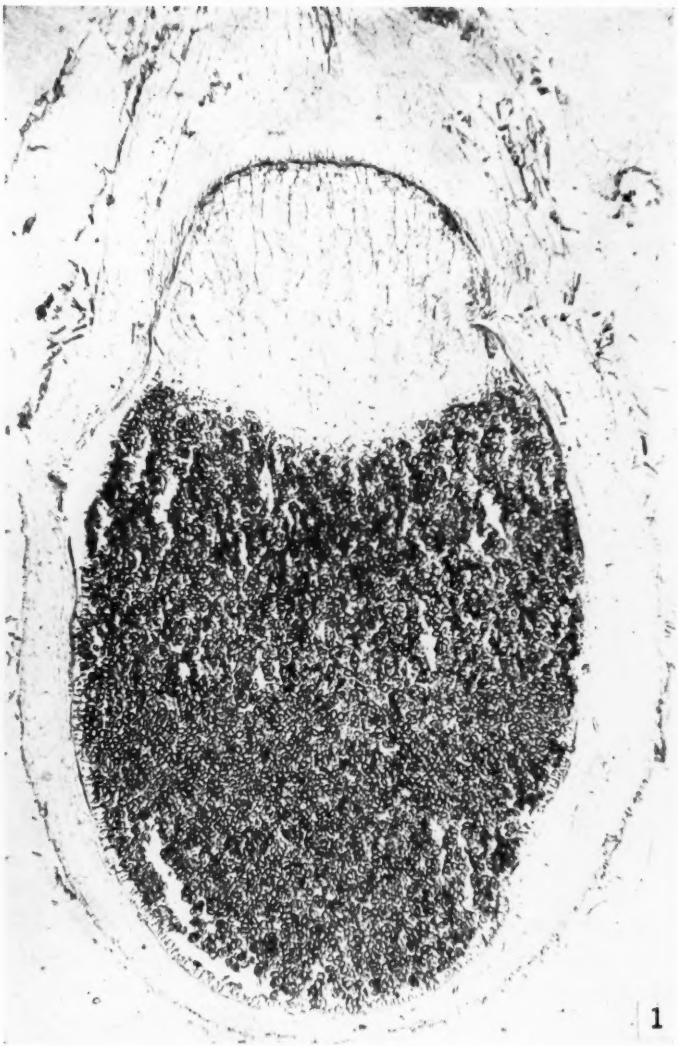


FIG. 1.*—Median longitudinal section through mature sporophyte of *Dumortiera hirsuta*.

* All drawings were made with the use of a camera lucida from living material and show uniform magnification of ×130.

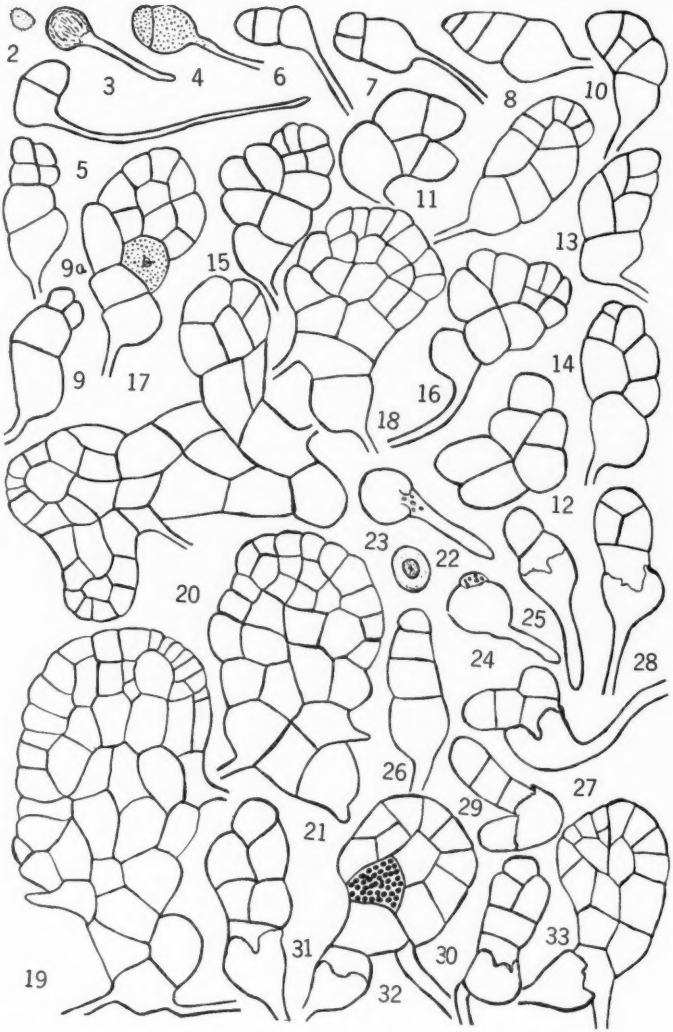
tion (**7**). In other species studied there was little or no distention of the spore before germination (**8, 9, 10**).

The first step in the germination process in the spore of *Dumortiera* is usually the emergence of a rhizoid, which is of particularly small caliber in this species, that is, in the sporelings and young gametophytes. The appearance of this primary rhizoid is followed by an unequal division of the spore cell. Cell division (or rather budding, inasmuch as each successive new cell is the result of an unequal division) continues until three or four cells in a linear series are formed (figs. 3–6, 8, 10). Then follow cell divisions at the tip of the filament, most often in an oblique plane, which give rise to an active, wedge-shaped, apical cell typical in the young developing gametophyte of the true ferns (figs. 13–16). This kind of cell division continues as the growth process advances, and it may occur in every cell of the original filament, the first cell only excepted (figs. 19–21). There are deviations from this more or less regular procedure, such as the early initiation of twin thalli (figs. 11, 20); or divisions in the second plane may occur early as in figures 7, 9, and 9*a*. Occasionally the primary rhizoid is much belated (fig. 21).

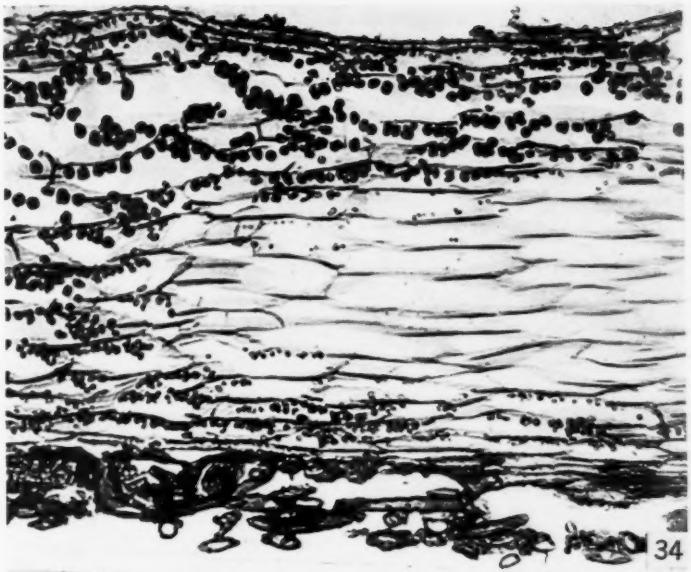
Besides the unusually small caliber of the rhizoids in the young gametophytes of *Dumortiera*, another distinctive feature is the exceptionally minute chloroplasts (fig. 17). In the adult thalli, however, the rhizoids seem to be as large as those of any of the other liverworts, and the chloroplasts are unusually large and plentiful (figs. 34, 35).

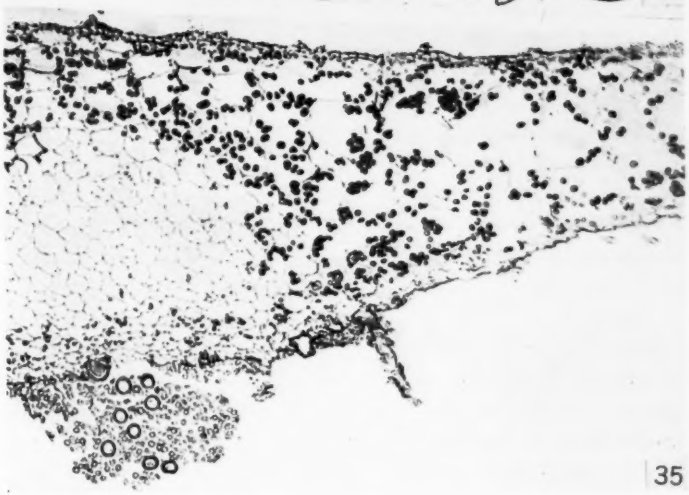
Comparison of Dumortiera and Onoclea struthiopteris

In tracing the development of the young thallus of *Dumortiera*, one is struck with the fernlike character of each figure. A comparison of the sporelings of *Dumortiera* with figures of *Onoclea struthiopteris* (**2**) showed the close resemblance between corresponding stages in the development of these two genera. Cultures of the spores of *Onoclea* were set up and typical stages were figured for comparison with those of *Dumortiera*. Unfortunately the cultures of these plants could not be grown simultaneously because spores of *Dumortiera* are viable for a few days only, after the dehiscence of the capsule, and the spores of *Onoclea* are not ripe until late autumn. There



FIGS. 2–33.—Figs. 2–6, 8, 10, 13–19, ripe spore and early stages in development of young gametophytes of *D. hirsuta;* figs. 7, 9–9*a*, 11, 12, 20, 21, young gametophytes of *D. hirsuta* which show irregularities in their development; figs. 22, 33, spore (with coat removed) and early stages in development of young prothallium of *Onoclea struthiopteris*.





FIGS. 34, 35.—Longitudinal and transverse sections through adult thallus of *Dumortiera hirsuta* showing non-chlorophyllose cells in thickest part of thallus.

was little difficulty, however, in matching practically all of the figures previously drawn of *Dumortiera* with the growing material of *Onoclea*. CAMPBELL considers *Onoclea* as typical of the Polypodiaceae, so that on this basis these results may be considered as representative for this group of ferns.

The regular procedure, including emergence of the primary rhizoid (fig. 23), transverse budding process followed by the oblique divisions, and early establishment of the cuneate apical cell (figs. 24–26, 28, 30, 31), is strikingly similar in *Dumortiera* and *Onoclea*. Even such irregularities as the introduction of twin thalli (fig. 27), the suppression of the primary rhizoid, and other early digressions (fig. 29) occur with about equal frequency in the two genera.

The chief morphological differences observed from the spores to the 13–20-celled stages in the gametophytes of these two species were: spore size, spore coats, diameter of the rhizoids, and number and size of the chloroplastids. The spore of *Onoclea* (fig. 22) is larger, increases relatively little before germination, and has a three-layered coat which is adherent even after the prothallium has assumed a definite heart-shape. The spore coat is early deciduous in *Dumortiera*. The chloroplasts in the young prothallium of *Onoclea* are several times as great in diameter as those of the young thalli of *Dumortiera* and are relatively fewer in number (figs. 17, 32).

Other differences noted in the two genera were more or less physiological and were beyond our control since the cultures of the two plants were not grown simultaneously. In general, the spores of *Onoclea* germinated more promptly, and more especially so in an atmosphere that was artificially heated, and the sporelings advanced more rapidly in north light than was the case in either the east or west exposures. The short daylight periods beginning November 4, the date on which the spores of *Onoclea* were sown, seemed to have no retarding effect; in fact, germination was equally prompt, if not more so, in cultures set up on December 10. Subsequent development of these young sporelings, however, was less than in the cultures started in November. Cultures placed in the south windows, one in a cool room and one in another kept at living-room temperature, gave negative results in the November sowings. Repetition of these tests in December showed germination in both cases, that in the warmer room being relatively much better. The optimum re-

sults of all of the spore germination experiments with *Onoclea* seemed to be in the warmer temperature (about 20° C.), on an average, in the north light exposure, and in (at least for development subsequent to germination) the longer daylight periods.

The conclusions drawn from these germination tests of the spores of the two genera are: that *Onoclea* can tolerate much less direct sunlight; needs at least moderate temperature; and seems to do well, probably best, in short daylight periods. *Dumortiera*, although also shade-loving, is more tolerant of direct sunlight and may need the longer daylight periods for its best expression in the matter of spore germination and subsequent development of the young gametophyte. At any rate, it seems that the season of long daylight is the only time at which spore germination could occur in *Dumortiera*, since its spores mature at this season and are ephemeral. It is likely too that a warmer temperature would have hastened germination in this exotic species. The spores of *Dumortiera* require about three weeks from the date of sowing to reach the 5–7-celled stage; those of *Onoclea* made similar progress in about half the time. Thus the differences observed in the germination process and in the development of the young gametophytes in *Dumortiera* and *Onoclea* are more physiological than morphological.

Campbell (2) compares the early schedule of cell division, etc., in *Onoclea* with the same processes in *Aneura*, which represents the simplest of the liverworts, and says that the early development of the gametophyte of *Marattia*, a primitive fern, is also much the same. On this basis *Dumortiera* may be considered primitive, at least in its method of thallus development. The relative simplicity of the adult gametophyte (figs. 34, 35) is also consistent with this theory.

Comparison of Dumortiera with some of its congeners

In the study of spore germination of six species of hepatics, *Marchantia polymorpha*, *M. domingensis*, *Conocephalum conicum*, *Preissia quadrata*, *Reboulia hemisphaerica*, and *Dumortiera hirsuta*, there seem to be four fairly distinct types, the *Marchantia-Preissia* type, the *Conocephalum* type, the *Reboulia* type, and the fern type which is represented by *Dumortiera*. The *Marchantia-Preissia* type bears considerable resemblance to the true ferns and therefore to *Dumortiera* in the early stages of the development of the gameto-

phyte, but shows much more irregularity in these early stages. And instead of the unequal division of the spore cell and the continuance of this budding process to form the short filament, these divisions in the *Marchantia-Preissia* type are more nearly if not entirely equal. Neither is it so easy to designate the apical cell in many of the young gametophytes of the *Marchantia-Preissia* type. MENGE (**5**), however, followed the complete development of individual sporelings of *Marchantia polymorpha* from the sowing of the spores to the fairly well advanced young gametophytes, and shows convincingly the activity of a 2-angled apical cell.

Conocephalum is probably unique among the Marchantiaceae with its intracapsular spore cell divisions up to the 30–40-celled stage before dehiscence of the capsule.

Reboulia initiates its thallus from a primordial group of cells which is invariably borne at the tip of a germ tube, whether this latter be of primary, secondary, or tertiary origin. MENGE presents results from the study of gametophyte development of *Plagiochasma* which bear marked resemblance to corresponding stages of spore germination and subsequent development of the young gametophyte of *Reboulia* (**9**). The adult thalli of these two genera are also remarkably similar in structure.

Dumortiera closely resembles the true ferns from spore germination to about the 18–20-celled stages, when the young prothallus of the fern begins to take on a definite heart-shape.

ADULT GAMETOPHYTES OF TYPICAL GENERA

An examination of the adult gametophyte of *Dumortiera* in both longitudinal and cross-sections (figs. 34, 35) shows the total absence of lacunae and the rather even distribution of the extraordinarily large chloroplasts throughout the tissues of the thallus, excepting in an area in the mid-region somewhat posterior to the tip (that is, in the thickest part of the thallus, there are no chloroplasts). Since chloroplasts are found ventral to this area, their absence in the middle portion of the thallus cannot be attributed to insufficient light. Perhaps these non-chlorophyllose cells are specialized to meet the greater conduction need in the thicker part of the plant.

Dumortiera has no ventral scales, despite the fact that these organs

are characteristic of the Marchantiaceae. CAMPBELL (2) says that there are none also in *Monoclea*, another aberrant genus which is closely allied to *Dumortiera*. The rhizoids, that is, those of the plain walled type, are of unusually large caliber in the adult thallus of *Dumortiera*, whereas those with pegged walls, although very numerous, are reduced in diameter.

Summary

1. *Dumortiera hirsuta*, probably one of two species only of this genus, is widely distributed in the tropics of both hemispheres and also in the more humid and warmer regions of the temperate zones.

2. The carpocephalum is covered with hairlike appendages and is borne on a stalk which has two groups of rhizoids on the side which corresponds to the ventral side of the thallus, this feature being the only suggestion of dorsiventrality in the stalk.

3. One or two sporophytes in each of the average number of eight groups of archegonia come to maturity. The sporophyte is made up of a rather indistinctly anchor-like foot, a massive columnar seta, and an ovate capsule which is depressed at the basal end. The whole is incased in a calyptra which is six cells in thickness.

4. The spores are ripe in Florida about the middle of April. They are viable for but a short time after the dehiscence of the capsule. The ripe spore is somewhat trihedral in form, is about 30 μ in its longest axis, and is surrounded by a golden brown papillate exine.

5. The elaters of *Dumortiera* resemble those of *Marchantia* in structure, size, and color; the proportionate number of spores and elaters agrees well with the condition in *Marchantia domingensis*.

6. The spores of *Dumortiera* germinate within six or seven days after being sown on a liquid medium. The first step in germination, following a considerable distention of the spore, is usually the emergence of a rhizoid followed by the formation of a bud from the spore.

7. The budding process most often continues until a short filament of three or four cells is formed. In the short filament of cells, divisions at the tip, usually in an oblique plane, result in the establishment of a wedge-shaped apical cell of the fern type. This zigzag type of cell production continues and may occur in every cell, the original cell only being excepted, as growth advances.

8. The young sporelings of *Dumortiera* are remarkably like those

of *Onoclea*, a typical Polypodiaceae, throughout the germination process and in the early stages of the development of the young gametophyte.

9. The adult thallus shows no lacunae and there is no definite line of demarcation between the chlorophyllose and the colorless cells, which latter are found in the more or less central part of the thallus; and there are no ventral scales on the thallus of *Dumortiera*.

10. *Dumortiera* may be considered an aberrant species because of the relative simplicity of the gametophyte; and the primitive features, such as the absence of ventral scales, lacunae, etc., are possibly only consistent with the history of the young gametophyte from the spore.

The writer is indebted to Dr. ROBERT G. GUTHRIE for the photomicrographic work for the illustrations in this paper.

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LITERATURE CITED

1. ANDERSEN, EMMA N., Morphology of sporophyte of *Marchantia domingensis*. BOT. GAZ. **88**:150–166. 1929.
2. CAMPBELL, D. H., The structure and development of mosses and ferns (Archegoniatae). 3d ed. Macmillan Co., New York. 1918.
3. ———, Studies on the East Indian Hepaticae. Ann. Botany **32**:319–329. 1918.
4. EVANS, A. W., A taxonomic study of *Dumortiera*. Bull. Torr. Bot. Club **46**:167–182. 1919.
5. MENGE, FRIEDRICH, Die Entwicklung der Keimpflanzen von *Marchantia polymorpha* L. und *Plagiochasma rupestre* (Forster) Stephani. Flora **124**: 421–476. 1930.
6. (O'HANLON) SISTER M. ELLEN, The germination of the spores of *Conocephalum conicum*. Amer. Jour. Bot. **7**:458–464. 1920.
7. ———, Germination of spores and early stages in development of gametophyte of *Marchantia polymorpha*. BOT. GAZ. **82**:215–22. 1926.
8. ———, A study of *Preissia quadrata*. BOT. GAZ. **84**:208–218. 1927.
9. ———, Gametophyte development in *Reboulia hemisphaerica*. Amer. Jour. Bot. **17**:765–769. 1930.
10. ———, Comparative morphology of *Marchantia domingensis*. (Unpublished.)
11. OWENS, OLIVE BOYD, Certain phases in the life history of *Dumortiera:* the development of the archegonium. Unpublished dissertation, Univ. of Chicago. 1927.

INFLUENCE OF SUPPLEMENTAL LIGHT ON BLOOMING

FRANCIS RAMALEY

(WITH THREE FIGURES)

This paper describes a series of studies carried on during each academic year from 1927 through 1933 to determine the effect upon plants of lengthened daily light exposure. Two Mazda lamps of 100 to 200 watt were placed in a reflector above the greenhouse bench, giving, at the height of the plants, from 15 to 30 foot-candle illumination. Since the greenhouse is well ventilated these lamps did not raise the temperature of the plants an appreciable amount. As a rule, artificial illumination of 5 foot-candles or less produces no visible effect, while 100 foot-candle illumination has little more influence than the 15 to 30 foot-candle illumination employed in these experiments. The moderate light here used could well be afforded by florists or others who might wish to hasten blooming of plants for commercial purposes.

One hundred species were employed for the investigation. The plants were grown in 5-inch pots, from 10 to 100 plants of each species being used in each case, always in four or more pots. When past the early seedling stage those which were to be irradiated were given artificial illumination from 5:00 until 10:00 P.M. or even all night. It makes very little difference in the time required for flowering in winter whether the day length is increased by supplemental light to 15, 20, or 24 hours.

The control plants, shaded from the artificial light, were placed on the bench a short distance from the experimental plants and were thus subjected to the same temperature and humidity. The greenhouse is not provided with automatic heat control, but an attempt was made to keep the rooms between 60° and 80° F. Since the temperature cannot be controlled during the summer the experiments were carried on only during the cooler months.

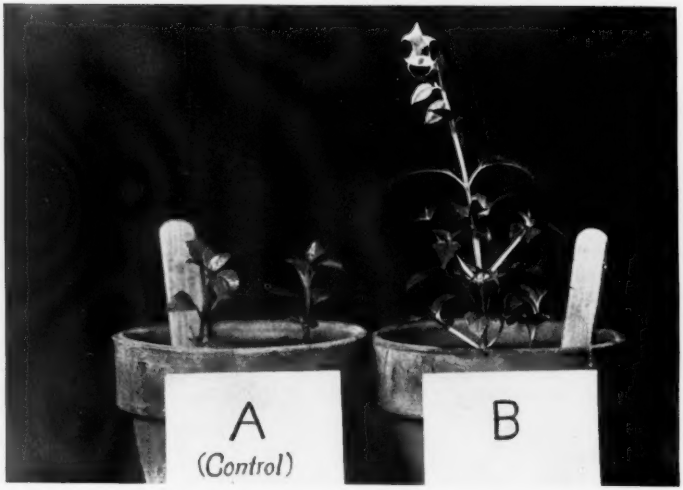

FIG. 1.—*Torenia fournieri*, a species hastened by supplemental light; planted Oct. 27, 1931: *B*, at right given supplemental light (30 foot-candles, continuous) from Feb. 26 to Apr. 7, when photographed.

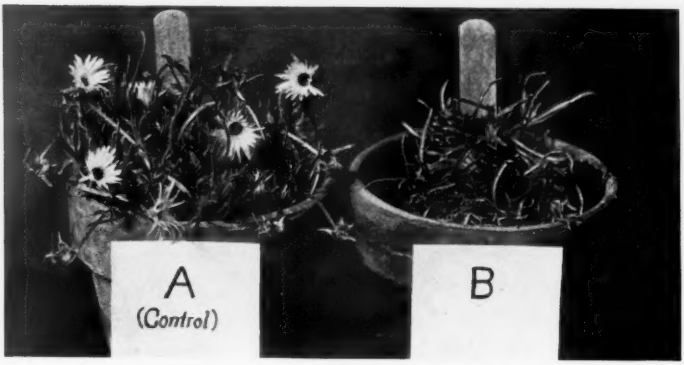

FIG. 2.—*Mesembryanthemum tricolor*, a species retarded by supplemental light; planted Oct. 31, 1931: *B*, at right, given supplemental light (30 foot-candles, continuous) from Dec. 5 to March 5, when photographed.

Observations

In nearly all cases the experimental plants grow taller, with lengthened internodes; and they often have appreciably thinner leaves and a slightly paler color than the controls. These etiolation effects are naturally to be expected because of the weak artificial light to which the plants are exposed for a time each day. An under-development of root system commonly occurs, with reduced

FIG. 3.—*Brassica alba*, planted Nov. 24, 1932; photographed Feb. 4, 1933: *A*, exposed only to daylight; *B*, exposed only to electric light (250 foot-candles, continuous); *C*, daylight plus supplemental light (30 foot-candles, continuous).

vascular tissue, especially phloem, while the stems tend to be lax. The leaves are not usually altered in size, but in a few instances are distinctly reduced. In radishes the hypocotyl elongates but does not swell to produce a "good radish." Red color of petioles and leaf midribs seldom develops even if present in the control series. No cases have been seen in which red or purple colors have appeared in the experimental plants when absent from the plants subjected to ordinary day length.

The most striking changes among the plants studied are in the time required until blossoming. Marked effects of increasing day

length appear in the winter months, while a few hours of extra illumination or even continuous 24-hour light has little influence in the long and hot days of summer.

As would be expected in view of the work of GARNER and ALLARD and many others,[1] some plants bloom quickly with lengthened illumination (long-day plants), some are delayed (short-day plants), while with others there is no marked difference between the experimental plants and the controls. Many plants have been tested in addition to those recorded in table I, and in none did the supplemental light affect to any extent either the vegetative or the reproductive activity.

Although exact dates of planting and blooming have been kept, it has seemed unnecessary to include them in the table, hence only the length of time required to bring the plants to blossom is given. The time of blooming is considered, not as the day on which the first single open flower is seen but the time when a considerable number of flowers have appeared. The localities named in the table are the native habitats, so that one may judge the length of day to which the species was originally exposed.

Certain species have been worked with during different years; in the table the results of the individual experiments are separately stated. These are often fairly consistent but sometimes are wide apart. Inconsistent results may be due to differences in time of year and in cultural care, or they may be of genetic origin, brought about by employing different horticultural varieties derived from diverse sources.

An asterisk in the table indicates that the plants did not bloom during the period of the experiment. The letters in the column following the names of plants have the following meanings: h, blooming hastened; r, blooming retarded; u, blooming unaffected.

[1] For further literature on the subject, see RAMALEY, F., A working bibliography of day length and artificial illumination as affecting growth of seed plants. Univ. Colorado Studies **20**: 257–263. 1933.

TABLE I

TIME FROM SOWING OF SEEDS TO BLOOMING, STATED IN NUMBER OF DAYS

SPECIES AND LOCATION	BLOOMING RESPONSE	EXPERIMENTAL PLANTS (DAYS)	CONTROL PLANTS (DAYS)
POACEAE			
Triticum aestivum var. Marquis (western Asia)	h	78	*
Zea mays (tropical America)	r	*	121
POLYGONACEAE			
Fagopyrum esculentum (central Asia)	u	70	70
CHENOPODIACEAE			
Atriplex hortensis (Eurasia)	u	91	91
Blitum capitatum (temperate North Africa)	h	93	171
AMARANTHACEAE			
Amaranthus sp.	r	163	71
" "		141	89
Celosia argentea (west Asia)	u	137	137
NYCTAGINACEAE			
Abronia umbellata (British Columbia to California)	h	120	153
AIZOACEAE			
Mesembryanthemum lineare (South Africa)	r	184	119
CARYOPHYLLACEAE			
Dianthus barbatus (Eurasia)	h	80	138
Dianthus caryophyllus (so. Eurasia to India)	h	162	182
" "		172	197
" "		133	144
Dianthus plumarius (Eurasia)	h	128	154
Gypsophila paniculata (Eurasia)	h	55	75
" "		48	83
" "		98	180
Lychnis coeli-rosa (Mediterranean)	h	70	160
Lychnis viscaria (Eurasia)	h	62	*
Saponaria "multiflora"	h	54	100
Silene vulgaris (Eurasia)	h	120	*
RANUNCULACEAE			
Adonis aestivalis (central Europe)	h	152	166
" "		115	135
Delphinium ajacis (south Europe)	h	91	135
Nigella damascena (south Europe)	h	79	119
PAPAVERACEAE			
Argemone sp. (southwestern United States)	h	102	150
Papaver rhoeas (Eurasia)	h	76	144
BRASSICACEAE			
Brassica alba (Eurasia)	h	48	90
" "		31	61
Iberis amara (Europe)	h	60	98
" "		89	131
Ionospidium acaule (Portugal)	u	61	61
Lobularia maritima (Mediterranean)	r	137	60
" "		62	62
Malcomia maritima (south Europe)	h	91	113
" "		69	90

TABLE I—*Continued*

Species and location	Blooming response	Experimental plants (days)	Control plants (days)
BRASSICACEAE—*Continued*			
Mathiola bicornis	h	104	118
Raphanus sativus var. French Breakfast (Mediterranean)	h	120	*
" " var. White Icicle (Europe)		90	139
CAPPARIDACEAE			
Cleome spinosa (tropical America)	r	125	95
RESEDACEAE			
Reseda odorata (north Africa)	h	124	134
" "		106	147
CRASSULACEAE			
Sedum coeruleum (Mediterranean)	h	132	182
MIMOSACEAE			
Mimosa pudica (Tropics)	u	197	200
CAESALPINACEAE			
Cassia chamaecrista (central United States)	h	82	103
FABACEAE			
Dolichos lablab (tropical Asia)	u	102	102
Lathyrus odoratus var. (Sicily) var. "Dwarf Cupid"	h	72	92
Lupinus perennis (southern U.S.)	u	121	121
Vicia faba (North Africa and southwest Asia)	u	71	75
TROPAEOLACEAE			
Tropaeolum majus (Peru)	u	60	60
" "		73	98
" "		61	75
EUPHORBIACEAE			
Euphorbia marginata (central United States)	r	184	155
" "		215	139
LIMNANTHACEAE			
Limnanthes douglasii (California to Oregon)	h	60	114
SAPINDACEAE			
Cardiospermum halicacabum (Tropics)	u	127	127
BALSAMINACEAE			
Impatiens balsamina (India, Malaya)	u	88	88
MALVACEAE			
Abutilon hybridum (Subtropics)	u	198	198
Lavatera trimestris (Mediterranean)	h	95	156
" "		103	129
" "		98	195
" "		103	185
VIOLACEAE			
Viola cornuta (Spain)	h	145	*
Viola tricolor (Europe)	h	82	210
" "		95	171
LOASACEAE			
Mentzelia lindleyi (California)	h	63	109
ONAGRACEAE			
Clarkia elegans (California)	h	109	127
Epilobium adenocaulon (New Brunswick to Colorado)	h	150	*
Godetia amoena (California to British Columbia)	u	71	85
" "		130	135

TABLE I—*Continued*

Species and location	Blooming response	Experimental plants (days)	Control plants (days)
APIACEAE			
Foeniculum vulgare (Europe)	h	102	122
Trachymene coerulea (Australia)	u	107	117
PRIMULACEAE			
Anagallis linifolia (Mediterranean)	h	108	207
PLUMBAGINACEAE			
Limonium sinuatum (Mediterranean)	u	100	100
APOCYNACEAE			
Vinca rosea (cosmopolitan in Tropics)	u	195	195
CONVOLVULACEAE			
Convolvulus tricolor (South Europe)	h	83	158
" "		67	101
" "		81	107
Ipomoea purpurea (tropical America)	r	300	61
Quamoclit coccinea (Tropics; Arizona, New Mexico)	u	135	64
" "		79	85
POLEMONIACEAE			
Collomia biflora (South America)	h	90	120
Gilia caespitosa (United States)	h	77	*
Phlox drummondii (Texas)	h	90	95
" "		77	125
HYDROPHYLLACEAE			
Nemophila menziesii (California, Oregon)	h	120	128
" "		52	102
Phacelia viscida (Southern California)	h	92	150
Phacelia whitlavia (Southern California)	h	63	125
BORAGINACEAE			
Echium plantagineum (south Europe)	h	66	112
Myosotis scorpioides (Eurasia)	h	43	95
VERBENACEAE			
Verbena hybrida (Argentina)	r	300	195
MENTHACEAE			
Salvia sp., var. Blue Beard	u	128	128
SOLANACEAE			
Browallia speciosa (Colombia)	u	174	174
Capsicum frutescens (tropical America)	h	105	125
Physalis pubescens (North America to Tropics)	u	115	110
Schizanthus wisetonensis (Chile)	h	66	113
" "		112	119
Solanum rostratum (North Dakota to Mexico)	r	157	106
SCROPHULARIACEAE			
Linaria maroccana (North Africa)	h	84	109
Nemesia versicolor (South Africa)	h	90	131
Torenia fournieri (Indo-China)	h	164	184
" "		147	147
ACANTHACEAE			
Thunbergia alata (tropical Africa)	u	83	83
RUBIACEAE			
Asperula orientalis (Eurasia)	h	50	132

TABLE I—*Continued*

Species and location	Blooming response	Experimental plants (days)	Control plants (days)
DIPSACACEAE			
Scabiosa atropurpurea (Eurasia, North Africa)	h	95	*
CUCURBITACEAE			
Citrullus vulgaris (tropical Africa)	u	82	82
Cucurbita pepo (Tropics)	u	54	54
Cucumis sativus (south Asia)	u	70	62
CICHORIACEAE			
Lactuca sativa var. longifolia (temperate Europe)	h	159	193
AMBROSIACEAE			
Xanthium commune (east and central United States)	r	152	53
CARDUACEAE			
Ageratum conyzoides (tropical America)	u	98	108
Brachychome iberidifolia (Australia)	h	139	153
Calendula officinalis (south Europe)	u	76	61
" "		79	79
Callistephus chinensis (China, Japan)	h	158	163
" "		150	170
" "		110	120
" "		146	154
" "		164	*
" "		144	182
Centaurea cyanus (southeastern Europe)	h	83	98
Chrysanthemum carinatum (North Africa)	h	99	135
" "		75	140
Coreopsis tinctoria (Ontario to central United States)	h	139	215
Cosmos bipinnatus (Mexico)	r	175	113
Dimorphotheca aurantiaca (South Africa)	h	84	129
Emilia flammea (New World Tropics)	h	99	110
" "		147	147
Gaillardia pulchella (Arkansas, Louisiana, Arizona)	h	159	218
" "		104	165
Helipterum manglesii (Australia)	h	83	105
" "		67	81
" "		66	76
Tagetes erecta (Mexico)	h	72	98
Tagetes patula (Mexico)	r	76	54
Zinnia elegans (Mexico)	u	*	83
" "		*	133
" "		85	85
" "		74	74

Discussion

It was hoped to discover in these studies an explanation for the different responses of the plants (table I), perhaps in the latitude of native habitat and consequent accustomed day lengths, or in their usual time of blooming whether in the long days of early summer

or in the shorter days of August and September. It might be that certain families would be found to show fixed reactions of a definite sort. But it must be confessed that no sweeping generalizations can thus far be drawn, and the results of experiments are presented now rather as interesting information. Of the 100 species with which this study deals, blooming was accelerated in 41, retarded in 12, not greatly affected in 27. Attention may, for one reason or another, be called to certain families and species. Further studies with these and with others not now mentioned may be expected to bring out other matters of interest. All of the eight species of the Caryophyllaceae thus far worked with have bloomed early when days are lengthened. A few perennial plants of various families were made to bloom in the first season by the use of supplemental light: *Lychnis viscaria*, *Silene vulgaris*, *Epilobium adenocaulon*, *Gilia caespitosa*. Among the plants which were not affected in their blooming or which were actually retarded by increased day length there is a rather large proportion of tropical species; while very few, perhaps not any, tropical species are much hastened in blooming by increased length of light exposure. A few of the species which are distinctly retarded in blooming by the lengthened day deserve mention: *Mesembryanthemum lineare*, *Euphorbia marginata*, *Xanthium commune*, *Cosmos bipinnatus*, *Tagetes patula*. In *Euphorbia marginata* the development of the characteristic white-edged leaves is greatly delayed.

Considerable preliminary experimentation has been carried on which is not recorded in the present paper. Numerous monocotyledons have been worked with, but most of them show no effects of supplementary light. Work has also been done with the common house plants and with most plants of vegetable gardens, but up to the present these species have furnished little of interest.

The studies here recorded are similar to those of the Purdue[2] and Ohio[3] experimenters whose papers were not received in time to be

[2] GREENE, LAURENZ, WITHROW, R. B., and RICHMAN, M. W., The response of greenhouse crops to electric light supplementing daylight. Bull. 366. Purdue Univ. Agric. Exp. Sta. pp. 1–20. 1932.

[3] LAURIE, ALEX, and POESCH, G. H., Photoperiodism: the value of supplementary illumination and reduction of light on flowering plants in the greenhouse. Bull. 512. Ohio Agric. Exp. Sta. pp. 1–42. 1932.

included in the bibliography previously mentioned. Certain of the plants used are the same in all three studies, and results are in general accord. The present writer, however, did not find a single species in which flowers were increased in size or number by the use of supplemental light. It seems highly unlikely on general biological grounds that such a result should be obtained, and it is probable that reports of such increase are based on too few cases to be of consequence.

The study discloses a number of species which do so well in the greenhouse when given supplemental light that they may be used for botanical class work in flower structure. Most noticeable are: *Triticum aestivum* (Marquis and other spring varieties), *Lychnis viscaria*, *Brassica alba*, *Malcomia maritima*, *Lavatera trimestris*, *Nemophila menziesii*, *Phacelia whitlavii*, *Callistephus chinensis*, and *Chrysanthemum carinatum*.

Summary

1. The effect of additional day length produced by artificial illumination during the winter months upon 100 species of greenhouse-grown (chiefly annual) plants is reported.

2. In practically all cases the experimental plants were taller, somewhat paler, less sturdy, and had a poorer root system than the controls.

3. The time from planting to blooming was shortened in 41 species, not greatly affected in 27 species, and lengthened in 12 species.

4. Of the plants hastened in blooming by supplemental light, most are natives of the temperate zone while those which showed no response were largely tropical. A few perennials were brought into blossom during the first season.

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PERSISTENCE OF SUBSPECIFIC TYPES OF XANTHIUM UNDER FIELD CONDITIONS[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 456

CHARLES A. SHULL

(WITH THREE FIGURES)

Although the genus *Xanthium* has been monographed twice in recent years (the North American species by MILLSPAUGH and SHERFF in 1919, and all known species of the world by WIDDER in 1923), it would be hard to find any group of plants in a worse state of taxonomic confusion. This statement is not meant as a criticism of the monographers working in this difficult field.

The number of species is not large. MILLSPAUGH and SHERFF (1) recognize twenty-one species in North America, while WIDDER (4) lists twenty-five for the entire world. He added MILLSPAUGH and SHERFF'S *X. curvescens* in an appendix, bringing the total to twenty-six species. But the two monographs have only seven species names in common; and two of these, *X. oviforme* and *X. strumarium* of MILLSPAUGH and SHERFF, are considered to be *X. saccharatum* and *X. indicum* by WIDDER instead of identical with his own *X. oviforme* and *X. strumarium*. Moreover, WIDDER'S *X. saccharatum* is considered synonymous with *X. pennsylvanicum* by MILLSPAUGH and SHERFF; and in turn, *X. pennsylvanicum* is considered a form of *X. pungens* by WIDDER. Six of MILLSPAUGH and SHERFF'S species are placed in *X. saccharatum* by WIDDER, and five others in *X. pungens*. No less than sixteen of the twenty-one species names used by MILLSPAUGH and SHERFF are considered but synonyms for other species by WIDDER.

It is only fair to say that the authors of these monographs had no opportunity to consult with one another during the progress of their work; nevertheless, one wonders how it is possible for such diversity of opinion to result from an examination of the same material. Under the circumstances one cannot speak with great certainty

[1] Read before the Illinois Academy of Science, East St. Louis, May, 1933.

about any particular species. There is much variability in the individual species apparently, and some natural crossing. The limits of variability need to be determined under severe tests, and the final revision of the genus may need to be based on a complete collection of all *Xanthium* types into some botanic garden where the habits of growth, responses to variable conditions, limits of variability, and hereditary characteristics for each form can be accurately observed.

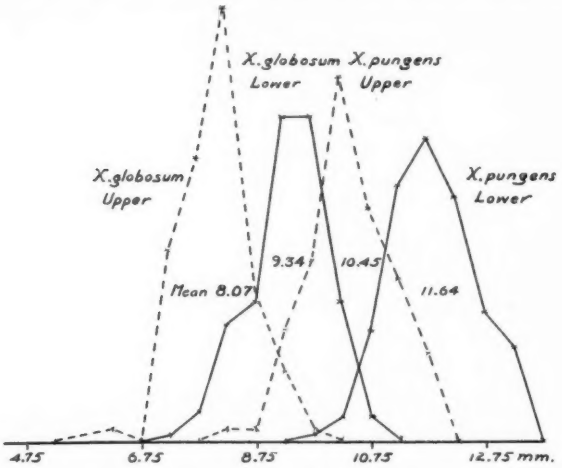

FIG. 1.—Curves of variability in length (in mm.) of upper and lower seeds of *X. globosum* Shull and *X. pungens* Wallr.

Several types of *Xanthium* have been observed in garden and field during recent years. One of these forms it was my good fortune to discover and name. *X. globosum* was first found near Lawrence, Kansas. It was grown for a number of years, and remained true to type generation after generation. MILLSPAUGH and SHERFF have given this form specific rank, while WIDDER, after examining it, calls it a variety of *X. pungens*, *X. pungens globosum*. A statistical study of the length, breadth, and weight of the seeds of *X. globosum* was made, in comparison with what WIDDER considers true *X. pungens*. In figure 1 is shown the curve of variability in length of the upper and lower seeds of *X. globosum* and *X. pungens*, based on the measurement of 200 seeds of each. There is almost no overlapping of

the curves. The curves of variability in breadth and weight show equally well the separation of these two forms. *X. globosum* has very dark colored, sleek, shiny seed coats, while the seed coats of WIDDER's *X. pungens* are dull grayish brown in color. In view of the fact that *X. globosum* differed in blooming time from *X. pungens;* differed in shape, color, and armature of bur; in color of seed, shape, length, breadth, and weight of seeds, it might well be given specific rank. It is able to maintain itself indefinitely under field conditions. Since it is controlled as to blooming time largely by photoperiodic responses, it tends to maintain its identity in the field, without excluding the possibility of crossing by wind pollination.

Another peculiar type of *Xanthium* which has been under observation for a number of years is the multiple-seeded form originally named *X. canadense globuliforme* by CREVECOEUR, but listed by MILLSPAUGH and SHERFF (**2**) as *X. chinense globuliforme*. It occurs sporadically in nature and may possibly be a hybrid; but if it is a hybrid it is of a non-splitting type. It reproduces itself year after year in the field, true to type, without any reversion and without any protection of any kind. Each bur usually contains five or six viable seeds. It is a vigorous grower, is enormously prolific (fig. 2), usually fasciated (or very much branched in lieu of fasciation), and is entirely unlike any other cocklebur in nature as to bur construction. While there are always a number of sterile blossoms in each bur, there are usually half a dozen fertile flowers, and no tendency has been noted toward a reduction of this number. If this type were permitted to escape, it could become a most serious pest. It is sturdy enough to maintain itself in severe competition with other weeds, and with other varieties of cockleburs. It will outgrow and outyield any other species of *Xanthium* found in the United States.

A third form which is considered of subspecific rank is a laciniate leaved form which has been described by SHERFF (**3**) as *X. pennsylvanicum laciniatum*. Similar laciniate forms are described by WIDDER as *X. orientale laciniatum*, *X. riparium laciniatum*, and *X. spinosum laciniatum*. This American laciniate leaved type was first found growing near Onaga, Kansas, by the late Mr. CREVECOEUR, and sent to me some years ago. It has been grown for four generations and has come fairly true to type. It is making itself at home in

FIGS. 2, 3.—Fig. 2 (upper), specimen volunteer plant of *X. canadense globuliforme* Crevecoeur, season of 1932. Fig. 3 (lower), specimen volunteer plant of *X. pennsylvanicum laciniatum* Sherff and Shull, season of 1932.

the field. Its offspring come up each year, and repeat the laciniate form of leaf (fig. 3). A test is in progress[2] at the present time to determine whether 100 per cent of the offspring are true to type, or whether a definite proportion of them revert to the ordinary field type of *X. pennsylvanicum*. Left to itself, there seems very little doubt of its ability to take and hold its place among other weeds, including those of its own genus, as a definite and permanent field type of *Xanthium*.

Such forms raise the whole issue of species concepts. What is the criterion or criteria of species? Should these true breeding forms be considered as mere varieties, or do they possess the necessary distinction and permanence to demand ranking as species? Taxonomists must ultimately settle this question. But unless there are some better standards than immature type and cotype materials stowed away in museums, we shall always have trouble in making a satisfactory classification. It is taxonomic heresy to throw away past work and begin all over again. But in this case, a collection of all species into a single garden might make possible a better definition of species. Ultimately an international congress might have to settle the status of the various true-breeding forms that are now considered of subspecific rank.

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LITERATURE CITED

1. MILLSPAUGH, C. F., and SHERFF, E. E., Revision of the North American species of *Xanthium*. Publ. no. 204. Field Museum of Natural History. 1919.
2. ———, *Xanthium*. North American Flora **33**:37–44. 1922.
3. SHERFF, E. E., New or otherwise noteworthy Compositae. VII. BOT. GAZ. **92**:202–209. 1931.
4. WIDDER, F., Die Arten der Gattung *Xanthium*. Repertorium specierum novarum regni vegetabilis. Beih. Bd. XX. Berlin. 1923.

[2] This test involved about 360 plants, the offspring of a single parent plant; 100 per cent of the progeny were laciniate leaved.

CALLIXYLON WHITEANUM SP. NOV., FROM THE WOODFORD CHERT OF OKLAHOMA

CHESTER A. ARNOLD

(WITH THREE FIGURES)

The material constituting the subject of this account comprises several pieces of silicified *Callixylon* wood which were collected by Dr. L. B. KELLUM in the Arbuckle Mountains during 1931. All are small specimens broken from larger trunks. None of the primary tissues in the central portions of the stems are included, so the description and the comparisons of this material with other types must be based upon secondary wood characters alone.

While the pieces at hand are small, they indicate having been broken from logs of considerable size. Very large logs as much as 5 feet in diameter are reported from the Woodford chert. These show that there must have been forest trees at the time of this deposition, comparable to the very large trees of *Callixylon newberryi*, the remains of which are common in the New Albany shale of Indiana and the Antrim shale of Michigan. It would seem, therefore, that both of these pre-Coal Measures species produced trees as large as those in a present day forest.

Since only the secondary wood is available, many of the anatomical features of *C. whiteanum* are unknown. It may be stated, however, that this wood presents no marked peculiarities or striking anatomical features, and as far as the width of growth rings, pitting, size of tracheids, etc., are concerned, this species shows but little to distinguish it from any of the better known forms, such as *C. zalesskyi* from the Genundewa limestone of New York or *C. newberryi* from the New Albany shale of Indiana. These forms have been previously described in some detail (**1**, **2**).

The problems of recognizing species from secondary wood characters are frequently stressed in anatomical literature and the difficulties as they apply to *Callixylon* have been previously discussed (**2**). After a detailed examination of several specimens of *C.*

newberryi, it became apparent that such features as thickness of the cell walls, number of pits per group, and width of the poorly defined growth rings usually visible in this wood are not clearly diagnostic and should be used to define species only after lengthy deliberation, and then with extreme caution. The regular distribution of the pits in radially aligned groups on the radial walls of the tracheids is a character confined, as far as the writer knows, to this genus. But the number of pits that make up the groups, or whether they are predominantly in one, two, or three rows per tracheid, are not in themselves characters that will clearly define a species. It should not be inferred from this that different species show no differences in these respects. *C. erianum*, for example, has groups with fewer pits on the average than *C. zalesskyi* or *C. newberryi*, but even here the extremes are about as great in one species as in the other. The number of rows of pits per tracheid is even of less significance, because this is definitely correlated with the size of the cells, and is not a specific character.

Vague growth rings appear to be present in all forms of *Callixylon*, and they can be seen in almost any specimen provided the block is large enough to include the very widely spaced ones. But the single fact that the rings in one block of wood may, for example, average 5 mm. in width and in another block 10 mm. has no specific significance where such variable characters are concerned.

The anatomical feature exhibited by *C. whiteanum* that appears to distinguish it is the structure of the rays as seen in tangential section. Most of the rays are entirely uniseriate, a few are partially biseriate, and occasional ones are entirely so. But the proportion of rays showing complete biseriation is small in proportion to the narrow ones. In *C. newberryi* fully one-half of the rays are completely biseriate. The resemblance to *C. zalesskyi* is much closer, and were the preservation of the latter such that this species could be studied in more detail, it is possible that the apparent differences between it and *C. whiteanum* could be interpreted as within the limits of variation of a single species.

It seems unadvisable to assign the Oklahoma material to *C. zalesskyi*, however, since it shows some features which appear to distinguish it. Furthermore, it comes from a horizon which is probably

distinct from the Genundewa limestone, and it is considered well to adhere to the usual practice of assigning new names to fossil plants of doubtful specific relationships and from distinct horizons. This is done, however, with the understanding that such nomenclature is tentative and subject to such modification as additional information upon the subject might require.

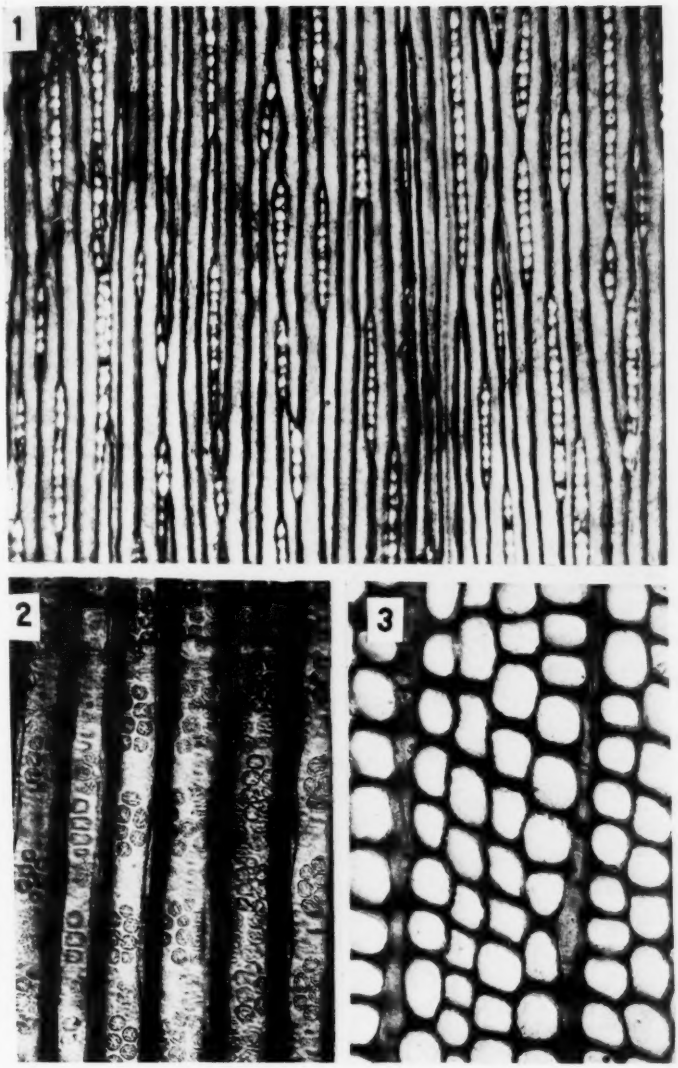
In *C. whiteanum* the rays range from a few (three or four) to seventy or eighty cells in height. The extremely high ones are rare and the majority of them are between ten and twenty-five cells. Such variations as this make concrete statement for the purpose of specific diagnosis rather difficult.

Ray tracheids have not been observed with certainty in *C. whiteanum*, but, judging from their occurrence in other species of the genus, it is altogether probable that they occur in all forms. Their sporadic occurrence in *C. newberryi* was unobserved until after a prolonged examination of exceptionally well preserved material. If such structures are present in the Oklahoma species they are inconspicuous in it also.

In naming this species, it seems appropriate to associate it with the name of Dr. DAVID WHITE, Principal Geologist of the United States Geological Survey.

Callixylon whiteanum sp. nov. (figs. 1–3)

DIAGNOSIS.—Arborescent; trunks large, several feet in diameter. Secondary wood gymnospermous, consisting of tracheids and rays; growth rings present but not strongly developed, irregularly spaced. Tracheids medium sized, varying from 30 to 70 μ in diameter, square or slightly elongated radially; thickness of wall between lumina of adjacent cells 6 to 11 μ. Bordered pits in one, two, or three (rarely four) rows on the radial walls of the tracheids; round or hexagonal or slightly appressed vertically if in a wall containing a single row; in radially aligned groups of few to many, but usually 5 to 15. Ray cells 4 to 20 μ wide, slightly higher; ray tracheids probably present but not clearly determinable. Rays mostly uniseriate but frequently biseriate in part or rarely biseriate for the entire height; few to many (75 or more) cells high. Extremely high rays rare.



FIGS. 1–3.—*C. whiteanum* sp. nov. Fig. 1, tangential section showing predominance of uniseriate rays, ×60; fig. 2, radial section showing disposition of pits in aligned groups, ×150; fig. 3, transverse section, ×125.

HORIZON AND LOCALITY.—Woodford chert (probably lower Mississippian), Arbuckle Mountains, Oklahoma (type, no. 15454, Museum of Paleontology, University of Michigan).

In comparing *C. whiteanum* with other known species of the genus, its closest resemblance as shown by the structure of the rays seems to be with *C. zalesskyi* from the Genundewa limestone of New York (1). This comparison is of necessity based upon secondary wood characters alone, and is subject to modification pending the discovery and description of the primary wood of the Oklahoma material. With the exception of the ray tracheids, which are abundant in *C. zalesskyi* but rare or absent in *C. whiteanum*, the general morphology of the rays is similar in the two forms. The pitting shows no features which serve as a basis for distinction.

As already explained, the scarcity of broad biseriate rays in *C. whiteanum* is the most pronounced difference between this species and *C. newberryi*. To the casual observer the similarity in preservation between the two species gives a superficial impression of likeness, which is seen not to exist after a careful microscopic examination. Being calcified instead of silicified, *C. zalesskyi* is in a much poorer state of preservation, and the similarity between this species and *C. whiteanum* is likely to escape the uncritical observer. Concerning size of tracheids, extent of the pit groups, etc., there are no appreciable differences between *C. whiteanum*, *C. newberryi*, and *C. zalesskyi*.

Certain resemblances between *C. whiteanum* and the Russian species, *C. trifilievi*, are noted. Examination of a few sections kindly supplied by the Cambridge Botany School shows the rays of the latter species to be predominantly small. It should be noted that in the original description of *C. trifilievi*, ZALESSKY (4) emphasized the small rays.

In a recent work on *Archaeopitys eastmanii*, SCOTT (3) calls attention to the fact that *Pitys*, *Callixylon*, and *Archaeopitys* constitute a unified group. It is unfortunate that the reproductive structures of none of these forms are known, for until then it will be impossible to determine the exact relationship of these forms to either the Cordaitales or the Pteridospermae. An intermediate position is suggested for *Callixylon* because of the diversity shown by the rays. Those

forms with wide rays, as *Pitys antiqua* and *C. newberryi*, suggest pteridospermic relationships, while other forms, as *C. trifilievi*, *C. whiteanum*, and *C. zalesskyi*, are more cordaitean.

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LITERATURE CITED

1. ARNOLD, C. A., The genus *Callixylon* from the Upper Devonian of central and western New York. Paper Michigan Acad. Sci. Arts and Lett. **11**:1–50. 1929 (1930).
2. ———, On *Callixylon Newberryi* (Dawson) Elkins et Wieland. Contrib. Mus. Paleont. Univ. Michigan **3**:207–232. 1931.
3. SCOTT, D. H., *Archaeopitys Eastmanii*. Ann. Bot. **47**:361–374. 1933.
4. ZALESSKY, M. D., Étude sur l'anatomie du *Dadoxylon Tchihatcheffi* Goepp. sp. Mém. Comité Géol. de Russe, N. S. **68**:29. 1911.

CHEMICAL COMPOSITION OF CERTAIN AQUATIC PLANTS

HORACE J. HARPER AND HARLEY A. DANIEL

In a previous paper[1] it was shown that the nitrogen content of the soil in ponds was an important factor in the development of a vigorous growth of aquatic vegetation, and since plants are an important link in the growth cycle of certain micro- and macro-organisms found in water, a further study of the composition of aquatic vegetation was made.

Composite samples of all plants which make up the major portion of the vegetation in ponds and lakes near Stillwater, Oklahoma, were collected in June, 1933. All of the plants were approaching maturity and should represent an average condition for this area. Analyses for total nitrogen, phosphorus, and calcium were made on the plant tissue after drying at 105° C., and the results are given in table I.

The nitrogen content of these plants was higher than that which is found in weeds and grasses, although a marked variation occurred in the total nitrogen content of the same kinds of plants secured from different locations. This difference was clearly demonstrated in case of *Potamogeton foliosus*, which was low in nitrogen when grown in sandy soil and high in nitrogen when grown in a dark colored soil higher in total organic matter. Similar results were secured with *Typha latifolia*. Data on the average composition of some common weeds and grasses are given in table II.

The average phosphorus content of the aquatic plants also was higher than that of ordinary forage produced from the growth of cultivated plants. This is an important factor since certain types of macro-organisms depend upon green plants for food, and plant material high in nitrogen, phosphorus, and calcium would be favorable from the standpoint of food supply. A considerable variation occurred in the phosphorus content in the same species, which might indicate the possibility of "luxury consumption" of this element by

[1] HARPER, H. J., Studies on the phosphorus content of certain Oklahoma waters and notes on the development of artificial ponds. Proc. Oklahoma Acad. Sci. 11. 1931.

plants growing on fertile soils, since there was no indication that the absence of other plant foods was restricting vegetative growth.

The data on the calcium content were unusual. All samples of *Elodea canadensis* were very high in calcium while all samples of

TABLE I

NITROGEN, PHOSPHORUS, AND CALCIUM CONTENTS OF AQUATIC PLANTS SECURED FROM LAKES AND PONDS NEAR STILLWATER, OKLAHOMA

No.	Species	Percentage		
		Nitrogen	Phosphorus	Calcium
1	Eleocharis	1.410	0.134	0.600
2	Elodea canadensis	1.675	0.231	10.800
3	Elodea canadensis	2.430	0.148	8.440
4	Elodea canadensis	1.990	0.196	8.650
5	Jussiaea diffusa	1.620	0.278	1.065
6	Myriophyllum pinnatum	1.840	0.121	5.920
7	Myriophyllum pinnatum	2.278	0.268	2.150
8	Nelumbo lutea	1.860	0.204	2.770
9	Nelumbo lutea	2.320	0.237	2.945
10	Potamogeton americanus	2.040	0.195	2.240
11	Potamogeton americanus	1.427	0.204	1.602
12	Potamogeton foliosus	2.520	0.492	2.800
13	Potamogeton foliosus	1.650	0.236	1.045
14	Potamogeton foliosus	2.125	0.226	2.765
15	Potamogeton foliosus	1.695	0.167	2.960
16	Potamogeton pectinatus	1.977	0.157	2.996
17	Sagittaria cuneata	2.250	0.220	1.045
18	Sagittaria cuneata	1.819	0.245	0.970
19	Typha latifolia	1.431	0.170	0.378
20	Typha latifolia	0.875	0.126	0.420
21	Typha latifolia	2.348	0.137	0.372
22	Typha latifolia	1.983	0.180	0.354
23	Typha latifolia	3.594	0.304	0.785
24	Spirogyra	1.420	0.131	4.625
25	Nodularia spumigena	2.794	0.364	2.100
26	Spirogyra	0.603	0.071	8.950

Typha latifolia were very low in this element. Incrustations on the leaves of *Elodea* plants may account in part for the high calcium content. The calcium content of aquatic plants may be an important factor in the clarification of water, since the water in ponds and lakes which contain no springs usually remains in a turbid condition for a

long period of time following periods of excessive rainfall, when no vegetation is present in the water, while the water in ponds and lakes containing vegetation clarifies rather quickly following rains, except during the winter months when biological activity is at a minimum. Further investigations on the effect of the calcium content of plants in relation to the clarification of turbid water is in progress.

Algae are commonly found in lake waters when the temperature of the water is not too high. Sample 25 in table I which was identi-

TABLE II

AVERAGE CONTENT OF TOTAL NITROGEN, PHOSPHORUS, AND CALCIUM IN SOME COMMON WEEDS AND MATURE GRASSES IN OKLAHOMA

No.	Species	No. of Analyses	Percentage		
			Nitrogen	Phosphorus	Calcium
1	Ambrosia artemisiaefolia	2	1.30	0.22	1.94
2	Andropogon furcatus	26	0.51	.08	0.27
3	Andropogon scoparius	43	0.61	.07	0.27
4	Erigeron canadensis	7	1.81	.27	0.98
5	Lactuca scariola	3	1.63	.28	1.82
6	Polygonum pennsylvanicum	1	2.54	.15	1.55
7	Sorghastrum nutans	6	0.83	.08	0.29
8	Syntherisma sanguinalis	5	1.46	0.19	0.36

fied as *Nodularia spumigena* was highest in total nitrogen. This sample was obtained from a pond which collects a considerable portion of its drainage from barn lots, and consequently the water was high in nitrogenous matter. Sample no. 24 was a spirogyra and was taken from a fish hatchery pond which had recently been fertilized with sheep manure containing a large quantity of alfalfa stems, both of which are high in nitrogen content. Sample no. 26 was also a spirogyra and it was lowest in total nitrogen. It was growing in a pool of water surrounded by sandstone rocks which were very low in phosphorus content, and this probably accounts for the small amount of phosphorus in these plants.

All of the algae were very high in calcium, and when algae are killed by the addition of copper sulphate to ponds and lakes, the organic matter begins to decompose, carbon dioxide production is accelerated, and the calcium compounds which are liberated are

available to flocculate clay particles which remain in suspension. When turbid waters do not contain vegetative plants which can easily be killed by the addition of small amounts of copper sulphate, treatment with this chemical does not increase the rate of settling of the colloidal material.

OKLAHOMA A. AND M. COLLEGE
STILLWATER, OKLAHOMA

BRIEFER ARTICLES

CHROMOSOMES OF THE SOY BEAN

(WITH ONE FIGURE)

The diploid chromosome number of *Soja hispida* (Mönch) has been reported as 40 by KARPETSCHENKO.[1] Since this species is very closely related to, if not identical with, the common soy bean *Soja max* (Piper), it was considered desirable to check the chromosome number of the latter by using a common variety. Numerous root tips and flower buds of several varieties were collected and passed through the usual killing and fixing processes, and stained with Haidenhain's iron-alum haematoxylin in an attempt to secure a cross-section of the proper stage of division. One was finally found, of a bud of the Illini variety, which carried several cross-sections of the metaphase of the reduction division of microsporogenesis. In figure 1 the haploid number of 20 chromosomes can be clearly distinguished; therefore the diploid number of 40 chromosomes in the Illini variety of *S. max* corresponds with that reported by KARPETSCHENKO for *S. hispida*.—COLLINS VEATCH, *Argo, Illinois.*

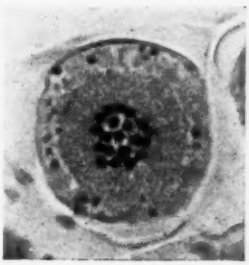

FIG. 1.—Cross-section of metaphase of reduction division of microsporogenesis. ×1600.

[1] KARPETSCHENKO, G. D., A report on the chromosomes in *Phaseolus*. Bull. Appl. Bot. and Plant Breed. (Leningrad) **14**:143. 1925.

CURRENT LITERATURE

Rusts

In a review of an earlier volume on the rusts by ARTHUR and associates, the reviewer stated that the value of the volume would have been greatly enhanced if a key and list of the known rusts had been included. Fortunately ARTHUR has been able to culminate a long and fruitful lifework with a manual[1] of the rusts in the United States and Canada.

The author aimed to produce a work "serviceable in the determination and collection of rusts by the general botanist," and to "present a classification showing the relation of species and genera as consistent with the present state of knowledge as lineal arrangement permits." In the main, the work abides by the International Rules of Botanical Nomenclature both for parasite and host; however, nomenclatural priority for the rusts is dated from 1753. The author also interprets the concept "perfect state" to be applicable to both uredinia and telia, thus conserving the names under the genus *Uredo* and avoiding substitution of 18 other names in the total of 694 species described. Pycnia and aecia are not recognized in matters of nomenclatural practice. In a few cases, however, the aecial names are used. ARTHUR systematically employs the terminology that he has advocated for designation of the various spore forms of the rusts and of their stromata. The preface includes a brief discussion of the relations of microcyclic (short cycle) and macrocyclic (long cycle) rusts.

An attempt is made to show degrees of relationship for the rusts other than that indicated by hosts. To this end genera are at times divided into sections, recognition of many more separate genera and species therefore being avoided. Species are aggregated "that exhibit correlation, that is, have sufficient points of resemblance to indicate descent from a common ancestor."

Biological and physiological species are not considered. The convention formulated by the American Phytopathological Society in 1925 is adopted as criterion of the species. Genetically, a species is a biological system in space-time characterized by reasonable continuity of interbreeding. So long as this test is not applicable to or has not been applied to the rusts, one convention is as permissible as another in delimitation and definition of species so long as it meets the pragmatic test of convenience and simplicity and is consistently carried out.

The volume is a finished piece of work, and treatment of the subject matter is consistent, precise, informative, and usable. The work represents the fruits of

[1] ARTHUR, J. C., Manual of the rusts in United States and Canada. pp. xv+438. figs. 487 and map. Purdue Research Foundation, Lafayette, Indiana. 1934.

a life's devotion to the subject, aided by the labors of many others. Its unity is that of one master mind. The value of the manual is enhanced by excellent indices of host and rust names, and by the excellent illustrations by G. B. CUMMINS. Publication was made possible by underwriting by the Purdue Research Foundation.—G. K. K. LINK.

Embryologie der Gymnospermen

The work represented by this volume[2] was undertaken originally by DR. STEPHANIE HERZFELD, who had assembled much of the literature and made many drawings, some of them ready for reproduction; but a long illness, ending with her death, came before there was any organization of the literature or writing of the book. Consequently, SCHNARF is responsible for practically the entire work.

The volume is organized under the following headings: male archesporium; formation of microspores; antheridial tapetum; pollen; ovule; female archesporium; macrospores; female gametophyte; female gametes; fertilization; embryo; time of year of various stages. Under nearly all of these headings the material is arranged in the following sequence: Cycadaceae, Ginkgoaceae, Taxaceae, Podocarpaceae, Araucariaceae, Cephalotaxaceae, Pinaceae, Taxodiaceae, Cupressaceae, Ephedraceae, Welwitschiaceae, and Gnetaceae. This organization makes it easy to use as a work of reference, and at the same time indicates the author's view of the rank and sequence of the various components of the gymnosperm phylum. In this feature SCHNARF has followed PILGER'S account in the second edition of ENGLER and PRANTL'S Die Natürlichenpflanzenfamilien.

While the book is largely a compilation, both in text and illustrations, the organization is excellent and the interpretation, in the opinion of the reviewer, is often more critical and comprehensive than in the original papers. This is doubtless because the author, in making such an extensive survey of the literature, was in a better position to interpret structures and to judge their significance in relation to the whole group.

The survey of the literature is so thorough that it reveals clearly where more work is needed. Consequently, investigators in favorable localities can easily secure material for study, especially since the closing chapter indicates the time of year for various stages in various regions. This feature, not only in this chapter but throughout the book, is so well presented that, knowing the time for one stage, like pollination, the times for other stages can be predicted with more or less probability. With this book for a guide, students in favorable localities can make their investigations very effective.

The book is a notable contribution to our knowledge of the life histories of gymnosperms and its place in the literature of the subject will be permanent.—C. J. CHAMBERLAIN.

[2] SCHNARF, KARL, Embryologie der Gymnospermen. Handbuch der Pflanzenanatomie, K. LINSBAUER. II. Abteilung 2. Teil: Archegoniaten, Band X/2. 8vo. pp. viii+303. figs. 467. Gebrüder Borntträger, Berlin. 1933.

Systematics of the Ascomycetes

The volume[3] under review is a product of a study begun in 1923 on the systematics of the Ascomycetes. In time the scope of the investigation was limited to a comparative study of Discomycetes, and finally to a study of the supposedly related Discomycetes and Disco-lichenes. The author concludes that the assumption of an extensive relationship between these two groups is erroneous. He proposes to designate the Disco-lichenes and the related Discomycetes as Lecanorales and to drop the term Disco-lichenes. Three main groups of higher Ascomycetes are recognized, and arranged in ascending series as follows: Plectascales, Ascoloculares, and Ascohymeniales. The latter includes, among others, the Discomycetes as its most primitive representatives and the true Pyrenomycetes. The author recognizes operculate and inoperculate Discomycetes, the latter including Lecanorales and the "non-lichenosi." The Lecanorales include the Ostropales (saprophytes) and the Helotiales (saprophytes and parasites). The Helotiales consist of six families, which include the vast majority of non-licheniate inoperculates. The major portion of the volume is devoted to a detailed taxonomic study of the Ostropales and Helotiales. This work is an important contribution to better systematization of the Ascomycetes and includes important theoretical considerations. The usefulness of the volume is greatly enhanced by figures and plates which are well done. There is a good bibliography and an excellent index.—G. K. K. Link.

Myxomycetes

A volume[4] devoted to a descriptive list of the known species of Myxomycetes, with special reference to those occurring in North America, has just appeared. It is in essence a revision of the senior author's The North American slime moulds, a standard since its appearance in 1922, enlarged to include the Myxomycetes of the world.

The introduction is devoted to discussion of general morphology, including basic definitions and concepts, and of collection and care of specimens. The material is organized on a taxonomic basis with keys to orders, each order with a family key, and each of these with a generic key. The synonymy of each species is given, adding to the value of the keys, and of the excellent descriptions of each species. The reported habitats are recorded.

The appendix lists names not included in the text, a valuable asset to the volume. The bibliography, while extensive, includes only the more important older works, a fuller list of recent articles on the morphology and physiology of the slime moulds, and lists relating to species distribution. The plates consist of

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[3] Nannfeldt, J. A., Studien über die Morphologie und Systematik der Nichtlichenisierten Inoperculaten Discomyceten. Nova Acta Regiae Societatis Scientiarum Upsaliensis. Ser. IV. Vol. VIII, no. 2. pp. 368. figs. 47. pls. 20. Almquist & Wiksells Boktryckeri, Upsala, Sweden. 1932.

[4] MacBride, T. H., and Martin, G. W., The Myxomycetes. pp. viii+339. pls. 21. Macmillan Co., New York. 1934.

573 illustrations executed by Miss GLADYS BAKER. They are well done and add to the usefulness of the volume. There is a good index. It is fortunate that the work of the senior author is being ably carried on by the junior author.—G. K. K. LINK.

Wound compensation, transplantation, and plant chimaeras

An extensive monograph[5] (no. 29 of the Monographien aus dem Gesamtgebiet der Physiologie der Pflanzen und der Tiere) has been prepared by KRENKE of the Timiriazeff Institute, Moscow, with the assistance of N. BUSCH, and O. MORITZ of the University of Kiel as translator and editor of the work. It is based on an earlier work, Chirurgie der Pflanzen, but so much enlarged and changed that it constitutes essentially a new work.

It is organized in two sections, the first of which (138 pp.) deals with the classification of mechanical influences which affect plants, especially the natural mechanical changes, such as tearing of tissues during normal growth, growth unions (ascidia, etc.), loss of dead or living organs, natural grafts, autotransplantations, formative fusion of tissues in stems and flower heads, and mechanical movements of structural parts such as the migration of nuclei, shifting of position of leaves, and the mechanical effects of wind.

The remainder of the work, which forms the second section, deals with artificial or chirurgic influences. Here are considered the reactions of cells and tissues to wounding, wound healing, regeneration following wounding, and wound compensations of all kinds. A lengthy consideration of transplantation and grafting experiments is given, and an interesting discussion of the physiological effects of stock and scion upon each other. Among these problems of graft partners and their mutual effects are such matters as the transport of organic substance and mineral nutrients from one to the other, changes in frost resistance, active acidity, influence of stock on offspring of scion, leaf color changes, changes in blooming time, effects of different ages of the grafted parts, and stimulus conduction through graft unions. In an appendix the serological relations of graft partners are considered. There is also a section on the practical value of grafting as a horticultural practice. The chapter on Chimaeras considers several types, such as graft chimaeras, stimulation chimaeras, chimaeras as a result of hybridization, and natural accidental and inheritable chimaeras. The last brief chapter considers the introduction of foreign bodies into plants, acquired immunities, internal therapy and related phenomena. The work brings together a very large body of information, and readers will appreciate the full knowledge which Professor KRENKE brought to his task. The literature citations occupy 34 pages. Several indices, genera and species names, authors, and subject matter, make it easy to find any particular information desired. It is, however, far too expensive.—C. A. SHULL.

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[5] KRENKE, N. P., Wundkompensation Transplantation und Chimären bei Pflanzen. 8vo. pp. xvi+934. figs. 203. Julius Springer, Berlin. 1933. RM. 88.

Studies of fossil Cycadophytes and Cycadofilicales based on epidermal characters

FLORIN's studies of the epidermis of living conifers have been followed by a volume of similar studies on Bennettitales and related groups.[6] The author shows how the shape of the stomata as well as of the epidermal cells can be used for taxonomic purposes. He shows that a reclassification of Bennettitales will be needed as soon as the available material of coalified leaves is sufficiently examined. FLORIN considers finely preserved coalified plant organs to be more satisfactory than petrifactions showing structure. It would be difficult to accept this statement were it not for the excellent photomicrographs which show his specimens.

A shorter paper by the same author[7] describes the stomata of a number of fossil Bennettitales.

The third paper by FLORIN, dealing with fossil Cycadophytes,[8] uses the cuticles for the description of a new species of Bennettitales. The author shows several photomicrographs of stomata at a magnification of 1000 times. They are very clear and so are photographs of hairs magnified 500 times.

Also in the case of Cycadofilicales, the FLORIN method can be used with great advantage, as he demonstrates in a short paper.[9]—A. C. NOÉ.

A new yearbook of botany

A new yearbook of botany,[10] somewhat similar to "Progressus rei Botanicae" but more comprehensive and compact, has made its appearance. Volume I reviews the botanical literature published in 1931; and volume II, that of 1932. Each of VON WETTSTEIN's collaborators is an outstanding investigator in his own field of botany, and the following list of chapter titles of volumes I and II, together with the author of each, gives an idea of the merit and scope of the work. (1) Morphology and evolution of cells, by L. GEITLER; (2) Morphology including anatomy, W. TROLL; (3) Phylogeny and reproduction, L. A. SCHLOSSER; (4) Taxonomy, J. MATTFELD; (5) Paleobotany, M. HIRMER; (6) Taxonomic and genetic plant geography, E. IRMSCHER; (7) Physico-chemical foundations of biologic processes, E. BRÜNNING; (8) Cellular and protoplasmic physiology, K. HÖFLER; (9) Water transport and movement of building substances, B. HU-

[6] FLORIN, R., Studien über die Cycadales des Mesozoikums nebst Erörterungen über die Spaltöffnungsapparate der Bennettitales. Kungl. Svenska Vetenskapsakademiens Handlingar. 3d Ser. **12**: 1–134. pls. 16. Stockholm. 1933.

[7] ———, Die Spaltöffnungsapparate der Williamsonia-, Williamsoniella- und Wielandiella-Blüten (Bennettitales). Arkiv Bot. **25A**: no. 15. pp. 20. Illustrated. Stockholm. 1933.

[8] ———, Über *Nilssoniopteris glandulosa* n. sp., eine Bennettitacee aus der Juraformation Bornholms. Arkiv Bot. **25A**: no. 20. pp. 19. Illustrated.

[9] ———, Zur Kenntnis der paläozoischen Pflanzengattungen *Lesleya* Lesquereux und *Megalopteris* Dawson. Arkiv Bot. **25A**: no. 19. pp. 23. Illustrated. Stockholm. 1933.

[10] Fortschritte der Botanik. Edited by FRITZ VON WETTSTEIN. Vol. I. pp. 263. Figs. 16. Julius Springer, Berlin. 1932. Vol. II, 1933.

BER; (10) Metabolism of mineral substances, K. MOTHES; (11) Metabolism of organic substances, A. RIPPEL; (12) Ecologic plant geography, H. WALTER; (13) Growth and movement, H. GUTTENBERG; (14) Inheritance, F. OEHLKERS; (15) Phylogenetic physiology, F. OEHLKERS; (16) Ecology, T. SCHMUCKER.

The critical treatment of material and the coherent and readable form in which it is presented distinguish the Fortschritte among abstracting journals. Its value is further enhanced by the promptness with which each issue covers the botanical literature of the preceding year.—A. C. NOÉ.

Phylogeny of conifers

A Danish botanist saw in a mountain forest of central Sumatra a peculiar conifer, *Dacrydium elatum*, whose male flowers resembled the strobili of *Lycopodium*. He preserved a large amount of material of the male and female reproductive organs and examined it upon his return to Denmark. The resulting publication[11] gives the interesting facts. He touches the questions of the relationship of conifers with the pteridophytes and the possibility that the conifers might represent the missing link between angiosperms and pteridophytes. The author tries to prove a connection between Lycopodiales and Cordaitales and between the latter and the Lycopodiales. He points to an apparent similarity between certain species of *Juniperus* and some primitive angiosperms. He constructs the following line of evolution: Psilophyta→Selaginellaceae→Lepidospermae→Cordaitales→Coniferae→(Angiospermae?).—A. C. NOÉ.

Textbook of systematic botany

In the six years since the appearance of SWINGLE's textbook, it has proved most serviceable in many laboratories, and this will guarantee a hearty welcome for a second edition.[12] There is no need to repeat here the favorable comments made in reviewing the earlier edition.[13] The pages of the new edition are enlivened by the addition of a number of illustrations, including the portraits of some of the botanical leaders of past generations.

The changes in the new edition are few and relatively unimportant. A few additions have been made, a few minor errors have been corrected, but the whole text remains essentially the same. This will be a matter of satisfaction to many teachers who have found the book useful.—G. D. FULLER.

Usefulness of wood in taxonomic descriptions

A series of articles which appeared recently in Tropical Woods illustrate the way in which the wood characters may be used for the description of plant fam-

[11] HAGERUP, O., Zur Organogenie und Phylogenie der Koniferen-Zapfen. Det. Kgl. Danske Videnskabernes Selskab. Biologiske Meddelelser. X, 7. pp. 82. Illustrated. Copenhagen. 1933.

[12] SWINGLE, D. B., A textbook of systematic botany. 2d ed. pp. xv+270. McGraw-Hill Co., New York. 1934.

[13] BOT. GAZ. **86**:115–116. 1928.

ilies, genera, and species. Very welcome is a glossary for the wood anatomist[14] which is comprehensive but terse. Another paper[15] explains in few words the value of wood anatomy in taxonomy. An excellent application of the characters of the wood for the systematic description of a family[16] illustrates a paper in a previous issue.—A. C. NOÉ.

Textbook of botany

A third edition of HOLMAN and ROBBINS' well known and widely used textbook of general botany[17] has recently been issued. The organization and plan of presentation remain essentially the same as in the previous editions, but such changes have been made by the authors as are justified by the advances of botanical knowledge since the publication of the second edition. The experience of the authors in the use of the book, together with suggestions from other teachers who have used it, have made it necessary to rewrite portions of every chapter. This has added to the clarity and value of the book as a general text while not increasing the number of pages appreciably. A number of the old illustrations have been redrawn or have been replaced by new ones, and there are about 50 additional figures.—J. M. BEAL.

Myrrh

A botanical and philological investigation about the source plant of the myrrh of the ancients[18] has been undertaken by an Egyptologist.

The author has compiled all available botanical information about plants that may have supplied the fragrant resin which was a greatly valued article of luxury in classical and biblical times. The myrrh of the ancients contained a volatile oil which was called στακτή (Stakte) by the Greeks. This was prepared from the resinous myrrh and had naturally the same source plant. The Egyptians called the resin cntjw.

The author thinks that the source plant might have been *Commiphora molmal* Engler, and suggests that resin of the living plant should be studied in order to establish beyond doubt the connection between the plant and myrrh. SCHWEINFURTH, who collected *C. molmal*, never saw it secrete the resin.—A. C. NOÉ.

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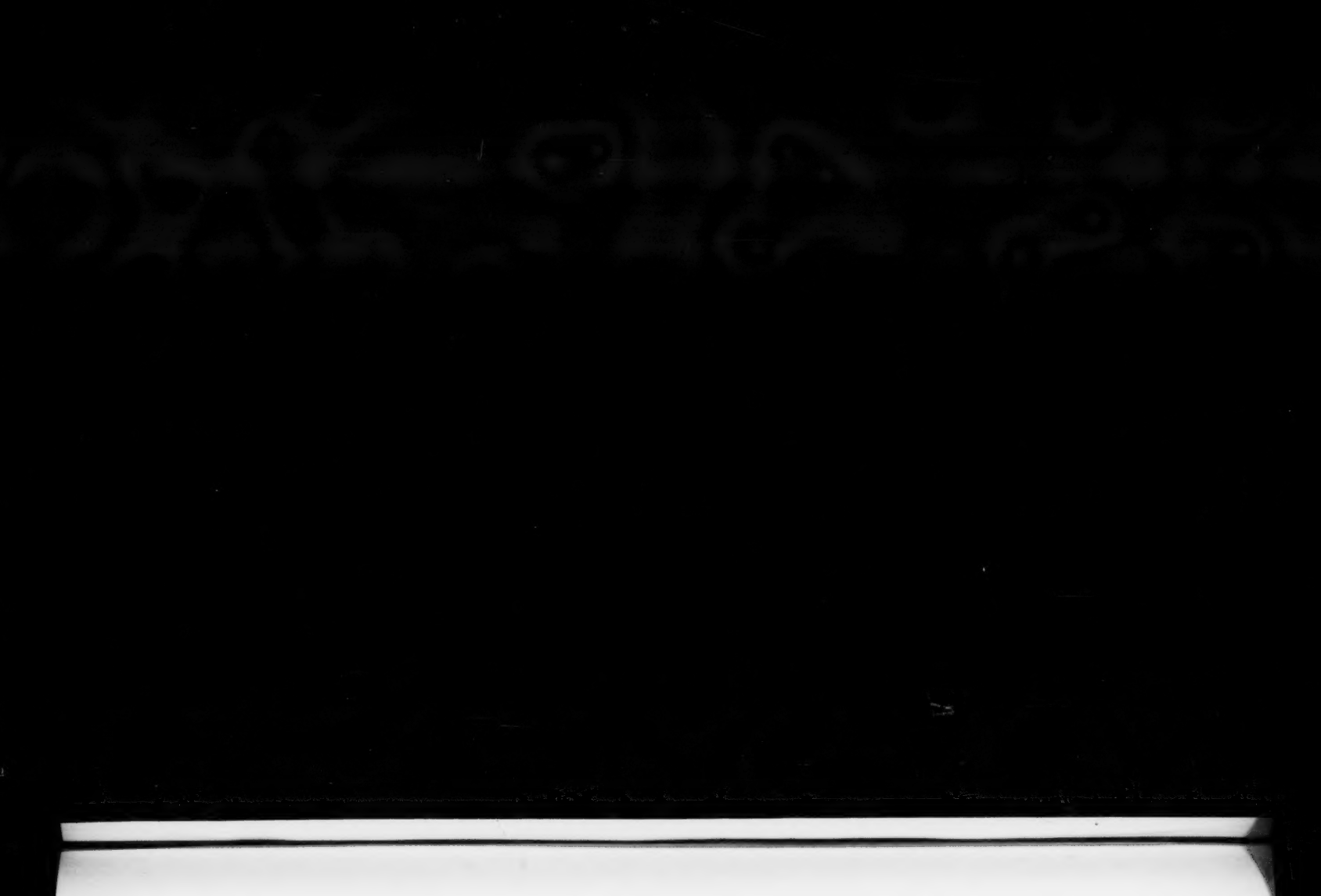
[14] COMMITTEE ON NOMENCLATURE, International Association of Wood Anatomists. Glossary of terms used in describing woods. Tropical Woods, Yale University, School of Forestry. pp. 1–12. No. 36, December, 1933.

[15] RECORD, S. J., Rôle of wood anatomy in taxonomy. Tropical Woods. pp. 1–9. No. 37, March, 1934.

[16] GARRATT, G. A., Systematic anatomy of the woods of the Myristicaceae. Tropical Woods. No. 35, September, 1933.

[17] HOLMAN, R. M., and ROBBINS, W. W., A textbook of general botany for colleges and universities. 3d ed. 8vo. pp. xv+626. figs. 463. John Wiley & Sons, New York. 1934. $4.00.

[18] STEUER, R. O., Myrrhe und Stakte. Wien, Verlag der Arbeitsgemeinschaft der Ägyptologen und Afrikanisten. pp. 48. 1933. RM 5.00.